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New physiologic races of the oat smuts[1]

GEORGE M. REED

In earlier publications I have described the occurrence of specialized races of both loose (*Ustilago Avenae* (Pers.) Jens). and covered (*U. levis* (K. & S.) Magn.) smuts of oats, which are distinguished by their different capacity for infecting oat varieties. The evidence recorded in the first paper (Reed, 1924) showed the existence of two distinct races of each of these smuts. The data were secured by the inoculation of several varieties of oats with a collection of each smut from Columbia, Missouri, and a second collection from Aberystwyth, Wales, which was sent to me by Miss Kathleen Sampson. The distinctive behavior of these two smuts was also confirmed by Miss Sampson (1925), who used them for inoculating several varieties of oats at the Welsh Plant Breeding Station. In a second paper (Reed, 1927), specialized races of loose smut which attacked Fulghum and Red Rustproof oats, belonging to the Red Oat Group, were described. These varieties had shown an unusually high degree of resistance to the other races, but Fulghum was severely attacked by collections of smut from Tennessee, Oklahoma, and Texas, and Red Rustproof by a different collection from Texas. Miss Sampson (1929) has recently recorded the occurrence of a new race of loose smut, characterized by its capacity for infecting *Avena brevis* and *A. strigosa*, and has also isolated another race of the covered smut. Rodenhiser (1928) has recorded differences in the cultural characteristics of collections of both loose and covered smut.

During the past few years I have been accumulating additional data on the general problem of physiologic specialization in the smuts of oats. A large number of collections of both loose and covered smuts have been obtained from various sources, and their capacity for infecting oat varieties has been determined. The result has been to demonstrate the existence of a large number of new races which can be distinguished by their varying ability to infect varieties of oats.

Extensive tests with my original collection of loose and covered smut from Missouri have been made on a large number

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of oat varieties (Reed, 1920; Reed, Griffiths, and Briggs, 1925). In the more recent studies, relatively few kinds of oats have been used, but they have served to show the main features of specialization. It is quite possible that if a larger number of varieties were grown in the experiments, additional evidence on the specialization of the various smut collections might be secured.

The methods employed have been similar to those used in previous studies. The inoculated plants have been grown to maturity, both in the greenhouse and in the field. Separate lots of seed were inoculated with the spores of the different smut collections. The inoculated seed was then planted in sand with a soil moisture of 20 per cent of its water-holding capacity, covered to a depth of about one inch, and germinated in a constant-temperature tank at 20°C. Earlier studies (Reed and Faris, 1924) have shown that these environal conditions are very favorable for securing high percentages of infection with the oat smuts. In most of the experiments, twenty seeds were planted in each container. The seedlings emerged ordinarily in four days and soon thereafter were transplanted to the greenhouse benches or to the field, where they were grown to maturity.

In most cases, two or more different experiments were carried out with each smut collection. Generally one or more series was carried to maturity in the greenhouse, and others in the field. The results, however, are combined in the tables. Since twenty seeds were usually inoculated in each experiment, the number of plants recorded in the tables indicates, to some extent at least, the number of different tests which were made with a particular variety and collection of smut.

It was usual to obtain high percentages of infection with varieties susceptible to a particular collection of smut. An examination of the tables will reveal the fact that frequently one hundred per cent of the inoculated plants were smutted. Every collection of each smut gave these high percentages with one or more oat varieties. Evidently favorable conditions for infection were secured, and thus the evidence for the specialization was conclusive.

In a number of the experiments only an occasional infected plant of a variety was observed. This may be accounted for

in different ways. For one thing, it is possible that an occasional seed was contaminated with smut from some unknown source. The fact that several collections of smuts were grown more or less adjacent to each other may account for some possible contamination. The second possibility is that an occasional stray seed of some variety was accidentally mixed with another and used in the planting. Usually, there was no way of detecting such mixtures, since the heads and grain of the infected plants were destroyed. There is also the third possibility that a resistant variety may, under exceptionally favorable conditions, be infected by a race of smut which ordinarily does not attack it. In a few cases we have conclusive evidence of this fact, since careful experiments have been tried out in which there was no possibility of accidental contamination of the seed or accidental mixtures of varieties.

PHYSIOLOGIC RACES OF USTILAGO AVENAE

The data for fifteen collections of loose smut are recorded in tables 1 to 5. In the tables 2 to 5 there are given the detailed results of the number of plants inoculated, the number infected and the percentage infected, while in the first table the combined results are given in order to show the peculiar behavior of the different varieties. One or more varieties or strains of seven different species of the genus *Avena* are included in these experiments, and the results indicate clearly the existence of a large number of specialized races of the loose smut.

A few general statements regarding the reaction of the different varieties to these collections of loose smut may be made. *Avena barbata* has proved to be exceedingly susceptible to all the collections with which it has been tested. Twelve of the fifteen collections have been used to inoculate this species, and in most cases one hundred per cent infection has been secured. The lowest percentage was obtained with Collection No. 4, in which 31 out of 49 plants (63.2 per cent) were infected.

One strain of *Avena brevis* was inoculated with all of the fifteen collections, and in every case proved to be entirely resistant; no infected plants were observed in any of the experiments.

Among the varieties of *Avena sativa*, two—Black Mesdag and Markton—stand out as completely resistant. Black Mes-

dag was tested with all fifteen collections, and Markton with all of them except No. 3, and no infected plants of either of these varieties were obtained in any of the experiments.

TABLE 1

Summary of results with Ustilago Avenae (Pers.) Jens.[a]

SPECIES AND VARIETY	SEED NO.	PHYSIOLOGIC RACE														
		I		II	III	IV		V	VI	VII	VIII	IX			X	XI
		Missouri	France	Kansas	France	Tunis	Germany	England	Germany	Wales	France	Tennessee	Oklahoma	Texas	Texas	France
		COLLECTION NUMBER														
		1	5	16	6	11	9	8	10	7	4	12	13	14	15	3
Avena barbata Brot.	830	5	5	—	—	5	—	5	5	5	4	5	5	5	4	5
Avena brevis Roth	289	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Avena nuda L.																
Hull-less	30	5	5	4	4	4	5	5	2	1	1	5	4	4	0	0
Liberty	292	5	4	5	5	4	5	5	0	0	0	2	2	3	0	—
Avena orientalis Schreb.	246	5	5	0	1	0	0	0	0	1	0	1	3	3	0	—
Green Mountain	110	5	5	5	5	5	5	0	1	0	0	—	—	—	—	—
Avena sativa L.																
Bicknell	341	2	1	—	1	4	1	1	1	1	1	5	3	5	1	—
Black Diamond	116	5	5	5	1	2	0	1	1	2	2	5	4	5	1	—
Black Mesdag	70	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black Norway	118	4	5	1	4	5	5	5	5	1	0	—	—	—	—	—
Canadian	119	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1
Early Champion	150	5	5	5	3	4	4	2	4	1	3	—	—	—	0	—
Early Gothland	152	5	4	1	1	0	0	1	0	1	0	0	3	3	0	0
Green Russian	316	4	3	5	0	0	0	0	1	0	0	0	1	2	—	—
Joanette	187	0	0	5	3	0	0	0	0	1	4	0	0	0	0	—
Markton	752	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—
Monarch	161	1	1	5	3	2	1	1	1	1	2	2	3	1	0	0
Monarch Selection	162	5	3	5	2	0	1	0	0	1	1	—	—	—	—	—
Nebraska No. 21	280	4	4	4	0	1	1	0	0	0	0	0	1	1	0	—
Rossman	322	5	3	0	1	0	0	1	0	1	1	0	2	1	—	—
Scottish Chief	124	3	3	4	3	4	4	3	0	1	0	1	2	1	0	0
Trisperma	64	5	4	5	5	5	5	5	4	0	0	4	1	3	0	—
Victor	126	5	5	5	5	5	5	5	5	5	5	5	3	4	1	2
Avena sterilis L.																
Burt	175	1	1	0	0	0	1	1	0	0	0	1	1	1	1	—
Fulghum	129	1	0	—	0	0	1	0	0	1	0	4	4	4	0	0
Navarro	946	0	—	—	—	—	—	—	—	0	—	0	0	0	0	—
Red Rustproof	131	0	0	0	0	0	0	1	0	0	0	0	0	0	4	0
Avena strigosa Schreb.	587	2	0	0	0	1	0	1	0	0	0	0	0	0	—	0

[a] In the body of this table numerals are used as symbols with the following significance:
— = No trial
0 = No infection
1 = 1–10 per cent
2 = 11–25 per cent
3 = 26–50 per cent
4 = 51–75 per cent
5 = 75–100 per cent

The other oat varieties inoculated gave quite different results with the various collections of smuts, and thus served to differentiate the specialized races.

Race I is based upon Collection No. 1. The original collection was made many years ago near Columbia, Missouri, and has been used in extensive experiments year after year. Its capacity for infecting a large number of varieties of oats

belonging to the various species has been determined, and most of them are more or less susceptible to this race of smut, relatively few being resistant (Reed, 1920; Reed, Griffiths, and Briggs, 1925). It has also been used in the earlier studies of physiologic specialization (Reed, 1924, 1927).

In the present experiments, only a few varieties or strains which seemed to be significant for the present purposes were included in the tests. Two varieties belonging to *Avena nuda*

TABLE 2

Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED NO.	*Avenae* NO. 1 Missouri			*Avenae* NO. 5 France			*Avenae* NO. 16 Kansas		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena barbata Brot.	830	38	38	100.0	18	17	94.4	—	—	—
Avena brevis Roth	289	84	0	0	53	0	0	20	0	0
Avena nuda L.										
Hull-less	30	126	116	92.0	96	75	78.1	37	27	72.9
Liberty	292	18	17	94.4	18	12	66.6	18	15	83.3
Avena orientalis Schreb.	246	104	102	98.0	71	54	76.0	37	0	0
Green Mountain	110	18	18	100.0	18	18	100.0	14	14	100.0
Avena sativa L.										
Bicknell	341	83	17	20.4	36	1	2.7	—	—	—
Black Diamond	116	52	46	88.4	14	14	100.0	17	15	88.2
Black Mesdag	70	102	0	0	78	0	0	20	0	0
Black Norway	118	53	30	56.6	19	18	94.7	16	1	6.2
Canadian	119	149	148	99.3	101	88	87.1	39	39	100.0
Early Champion	150	20	20	100.0	37	37	100.0	39	39	100.0
Early Gothland	152	127	121	95.2	77	51	66.2	40	1	2.5
Green Russian	316	55	34	61.8	35	15	42.8	20	19	95.0
Joanette	187	65	0	0	35	0	0	39	34	87.1
Markton	752	50	0	0	47	0	0	20	0	0
Monarch	161	145	1	0.6	93	2	2.1	55	51	92.7
Monarch Selection	162	53	47	88.6	40	20	50.0	39	33	84.6
Nebraska No. 21	280	43	31	72.0	52	29	55.7	38	25	65.7
Rossman	322	58	57	98.2	43	20	46.5	20	0	0
Scottish Chief	124	125	39	31.2	76	36	47.3	40	27	67.5
Trisperma	64	62	52	83.8	27	16	59.2	18	15	83.3
Victor	126	106	105	99.0	76	59	77.6	20	20	100.0
Avena sterilis L.										
Burt	175	52	2	3.8	44	2	4.5	10	0	0
Fulghum	129	87	3	3.4	57	0	0	—	—	—
Navarro	946	17	0	0	—	—	—	—	—	—
Red Rustproof	131	98	0	0	63	0	0	18	0	0
Avena strigosa Schreb.	587	94	19	20.2	76	0	0	18	0	0

were inoculated, and both proved to be highly susceptible. The same is true of the two varieties of *A. orientalis*. Seventeen varieties of *A. sativa* have been grown in the various experiments. In addition to Black Mesdag and Markton, two others stand out as distinctly resistant, namely, Joanette and Monarch. No infected plants of the former have been observed, while only one, in a total of 145 of the latter, has been obtained. The other varieties used have given comparatively high percentages of infection, the lowest being secured with Bicknell

(17 infected plants out of a total of 83, or 20.4 per cent) and Scottish Chief (39 infected plants out of a total of 125, or 31.2 per cent).

This race has shown very slight capacity for infecting the varieties of the Red Oat Group, tests having been made with Burt, Fulghum, Navarro and Red Rustproof. Usually, entirely negative results have been secured, but occasionally a plant of Burt and Fulghum has been infected. The varieties of this group, however, stand out as strikingly resistant to this race of smut.

Several varieties of *Avena strigosa* have been tested with this race, but only one of them, belonging to the subspecies *glabrescens*, has been used in comparison with the other collections of loose smut. This strain has given very variable results with this race. In one experiment, a relatively high percentage of infection was obtained, while in four others, negative results were secured.

Another collection of loose smut, No. 5, has given results which closely parallel those just described. The original material of this collection was obtained by Dr. C. R. Hursh in June 1924 near Noisy de Roi, France. It has been tested out on all of the species and varieties except Navarro, and its behavior corresponds very closely with that of Collection No. 1. The only obvious difference is its failure to infect Bicknell and *Avena strigosa*. With the former variety, two tests were made in the field and only one plant out of 36 was infected. However, under similar conditions, Collection No. 1 gave practically negative results on this same variety. Four tests have been made with *A. strigosa*, and in no case did any infection occur. On the other varieties and species the collection behaved like No. 1.

Race II is based on Collection No. 16. The material was collected at Hays, Kansas, in 1925 by Mr. F. A. Coffman and forwarded to me by Mr. T. R. Stanton. Office of Cereal Crops and Diseases, U. S. Department of Agriculture. According to the original information, the smut was collected on the Burt oats. The smut, however, has shown no special capacity for infecting Burt oats or other varieties belonging to the *Sterilis* Group. However, the number of tests and plants of these varieties grown in the experiments was quite small.

The smut, however, stands out clearly from Race I. It infects severely both varieties of *Avena nuda* and Green Mountain, a Side Oat type, the other variety of this group giving entirely negative results. Three varieties of *A. sativa*, in addition to Black Mesdag and Markton, namely, Black Norway, Early Gothland, and Rossman, gave practically negative results. The other varieties tested usually gave high percentages of infection.

From the positive standpoint, the outstanding features of this race are its capacity to infect Joanette and Monarch, two varieties completely resistant to Race I. With Joanette, 34 out of 39 plants (87.1 per cent) and with Monarch, 51 out of 55 plants (92.7 per cent) were infected. On the negative side, as already noted, it has failed to infect such varieties as Orientalis (Seed No. 246), Black Norway, Early Gothland, and Rossman, varieties which have usually given very high percentages of infection with Race I. *Avena strigosa* has also given entirely negative results.

Race III is based on Collection No. 6. The material was originally collected by Dr. Hursh in the same locality as collection No. 5. The evidence is clear, however, that it is a distinct race. It has proved capable of infecting both varieties of Hull-less oats. It has also severely infected Green Mountain, but the other Side Oat type gave practically negative results. Among the varieties of *Avena sativa* some, as Early Gothland, Green Russian, Nebraska No. 21, and Rossman, gave practically no infection; other varieties, as Bicknell, Black Diamond, Early Champion, Monarch Selection, and Scottish Chief, gave relatively few infected plants. Severe infection of Joanette and Monarch was secured, and in this respect the race corresponds with the one previously described. It differs from this race, however, in its ability to infect Black Norway and also in giving practically negative results on Black Diamond. The varieties belonging to *A. sterilis* and *A. strigosa* all have proved to be resistant to it.

Race IV is based on Collection No. 11. This was originally secured from contaminated oat seed received from Tunis. It also produces severe infection on the two varieties of the Hull-less Group and the Side Oat, Green Mountain. It is negative on Orientalis (Seed No. 246) and also on Early Goth-

land, Green Russian, Joanette, Monarch Selection, and Rossman. It has severely infected Bicknell, Black Norway, Canadian, Early Champion, Scottish Chief, Trisperma, and Victor; Black Diamond, Monarch, and Nebraska No. 21 gave comparatively low percentages of infection. It has also proved negative on the varieties of the *Sterilis* Group and *Avena strigosa*. It is very similar to Race II; it differs, however, in infecting much more severely Bicknell, less severely Monarch, and not at all infecting Joanette.

TABLE 3

Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED NO.	*Avenae* NO. 6 France			*Avenae* NO. 11 Tunis			*Avenae* NO. 9 Germany			*Avenae* NO. 8 England		
		No. pl.	No. inf.	% inf.	No. pl.	No inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena barbata Brot.	830	—	—	—	15	15	100.0	—	—	—	25	25	100.0
Avena brevis Roth	289	36	0	0	50	0	0	34	0	0	79	0	0
Avena nuda L.													
Hull-less	30	83	44	53.0	99	52	52.5	81	65	80.2	147	113	76.8
Liberty	292	18	14	77.7	19	12	63.1	18	14	77.7	20	18	90.0
Avena orientalis Schreb.	246	91	1	1.0	66	0	0	65	0	0	85	0	0
Green Mountain	110	18	17	94.4	18	18	100.0	18	18	100.0	16	0	0
Avena sativa L.													
Bicknell	341	30	3	10.0	39	27	69.2	32	1	3.1	29	1	3.4
Black Diamond	116	34	3	8.7	15	2	13.3	16	0	0	38	1	2.6
Black Mesdag	70	71	0	0	69	0	0	54	0	0	126	0	0
Black Norway	118	19	14	73.6	19	15	78.9	19	15	78.9	18	16	88.8
Canadian	119	90	88	97.7	99	93	93.9	69	69	100.0	137	134	97.8
Early Champion	150	39	12	30.7	40	30	75.0	36	26	72.2	37	4	10.8
Early Gothland	152	99	1	1.0	71	0	0	57	0	0	127	2	1.5
Green Russian	316	49	0	0	35	0	0	28	0	0	55	0	0
Joanette	187	40	17	42.5	37	0	0	37	0	0	36	0	0
Markton	752	57	0	0	39	0	0	46	0	0	42	0	0
Monarch	161	91	39	42.8	94	13	13.8	62	2	3.2	128	5	3.9
Monarch Selection	162	38	5	13.1	38	0	0	38	2	5.2	39	0	0
Nebraska No. 21	280	48	0	0	51	4	7.8	48	4	8.3	51	0	0
Rossman	322	40	1	2.5	40	0	0	39	0	0	34	1	2.9
Scottish Chief	124	96	34	35.4	71	47	66.1	78	57	73.0	117	55	47.0
Trisperma	64	28	28	100.0	20	19	95.0	22	22	100.0	14	12	85.7
Victor	126	74	70	94.5	72	56	77.7	54	49	90.7	100	93	93.0
Avena sterilis L.													
Burt	175	61	0	0	46	0	0	35	3	8.5	53	1	1.8
Fulghum	129	79	0	0	76	0	0	58	1	2.6	131	0	0
Red Rustproof	131	76	0	0	34	0	0	53	0	0	111	1	0.9
Avena strigosa Schreb.	587	46	0	0	57	1	1.7	36	0	0	89	4	4.4

Another collection, No. 9, has given results very similar to those obtained with No. 11. It was sent to me originally by Dr. Theo. Roemer, University of Halle, Germany, from material secured at Leipzig, Germany. It differs from the previous collection by its failure to produce a severe infection on Bicknell, otherwise it runs quite close to this collection. It stands out from Race II by its infection of Black Norway and the negative results obtained with Joanette and Monarch.

Race V is based upon Collection No. 8. The original material was sent to me by Dr. George H. Pethybridge, having been collected in August 1924 at Somerset, England. It is very similar to Race IV, but differs distinctly from that one in its inability to infect Green Mountain and Early Champion. These two varieties have usually given high percentages of infection with the races already described. With this race, however, only 4 plants out of 37 of Early Champion were infected, and none out of 16 of the Green Mountain. Practically negative results have been obtained with the oats of the *Sterilis* Group, and only 4 plants out of 89 of *Avena strigosa* have been infected.

Race VI is based upon Collection No. 10. The original material was sent to me by Dr. Roemer, having been made at Dahlem, Germany. The race is distinguished by the fact that it is incapable of producing severe infection of the Hull-less oats. Green Mountain and Orientalis (Seed No. 246) also gave practically negative results. A considerable number of varieties of the *Sativa* Group of oats also proved to be resistant to this race; in fact, it proved to be capable of severely infecting only the varieties Black Norway, Canadian, Early Champion, Trisperma, and Victor. The results were negative on the *Sterilis* varieties and *Avena strigosa*.

Race VII is based upon Collection No. 7. The data recorded in the table were secured from material received from Dr. Pethybridge who, however, obtained it from Miss Sampson in Wales. The smut is identical with that previously used in my experiments and supplied direct by Miss Sampson. The race stands out from those previously described by its failure to infect *Avena nuda* and *A. orientalis*. Many varieties of *A. sativa*, including Bicknell, Black Diamond, Black Norway, Early Champion, Early Gothland, Green Russian, Joanette, Monarch, Monarch Selection, Nebraska No. 21, Rossman, Scottish Chief, and Trisperma, proved to be negative; in fact, only two varieties—Canadian and Victor—showed any high degree of susceptibility to this race. *Avena sterilis* and *A. strigosa* have also given essentially negative results.

Race VIII is based upon another collection, No. 4, made by Dr. Hursh at Lambesc, France, in June 1924, and has given results very similar to those described for Collection No. 7.

It has run fairly parallel to it in its behavior with reference to the varieties. The only outstanding difference is its capacity for infecting Joanette; 26 out of 37 plants (70.2 per cent) of this variety were infected, while only 2 out of 35 plants (5.7 per cent) were infected with the previous collection. Early Champion and Monarch also have given somewhat higher percentages of infection. *Avena sterilis* and *A. strigosa* have proved negative.

TABLE 4

Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED NO.	*Avenae* NO. 10 Germany			*Avenae* NO. 4 France			*Avenae* NO. 7 Wales			*Avenae* NO. 3 France		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena barbata Brot.	830	15	14	93.3	49	31	63.2	24	24	100.0	36	36	100.0
Avena brevis Roth	289	36	0	0	77	0	0	84	0	0	49	0	0
Avena nuda L.													
Hull-less	30	80	12	15.0	125	2	1.6	150	2	1.3	48	0	0
Liberty	292	19	0	0	16	0	0	18	0	0	—	—	—
Avena orientalis Schreb.	246	67	0	0	73	0	0	78	1	1.2	—	—	—
Green Mountain	110	14	1	7.1	16	0	0	14	0	0	—	—	—
Avena sativa L.													
Bicknell	341	38	2	5.0	40	1	2.5	30	2	6.6	—	—	—
Black Diamond	116	18	1	5.5	19	4	21.0	37	5	13.5	—	—	—
Black Mesdag	70	55	0	0	107	0	0	133	0	0	48	0	0
Black Norway	118	19	18	94.7	16	0	0	19	1	5.2	—	—	—
Canadian	119	70	67	95.7	125	125	100.0	182	175	96.1	49	1	2.0
Early Champion	150	36	19	52.7	37	13	35.1	39	1	2.5	—	—	—
Early Gothland	152	69	0	0	98	0	0	141	1	0.7	27	0	0
Green Russian	316	35	3	8.5	35	0	0	44	0	0	—	—	—
Joanette	187	38	0	0	37	26	70.2	35	2	5.7	—	—	—
Markton	752	56	0	0	43	0	0	51	0	0	—	—	—
Monarch	161	73	5	6.8	118	22	18.6	151	1	0.6	41	0	0
Monarch Selection	162	38	0	0	40	3	7.5	56	2	3.5	—	—	—
Nebraska No. 21	280	54	0	0	51	0	0	51	0	0	—	—	—
Rossman	322	38	0	0	39	1	2.5	40	3	7.5	—	—	—
Scottish Chief	124	74	0	0	96	0	0	142	1	0.7	19	0	0
Trisperma	64	24	17	70.8	29	0	0	20	0	0	—	—	—
Victor	126	62	53	85.4	85	79	92.9	118	98	83.0	19	2	10.5
Avena sterilis L.													
Burt	175	43	0	0	50	0	0	67	0	0	—	—	—
Fulghum	129	35	0	0	85	0	0	97	1	1.0	50	0	0
Navarro	946	—	—	—	—	—	—	12	0	0	—	—	—
Red Rustproof	131	52	0	0	86	0	0	98	0	0	28	0	0
Avena strigosa Schreb.	587	56	0	0	103	0	0	95	0	0	46	0	0

Race IX is based upon Collection No. 12, which was obtained from Dr. L. R. Hesler, University of Tennessee, Knoxville, Tennessee, in the summer of 1924. The special feature of this collection is its capacity to infect the Fulghum oats of the *Sterilis* Group. Seven different strains of these oats, including Frazier and Kanota, have been tested in two or more experiments. The percentage of infection has varied from 62.5 to 82.7, and in some of the individual experiments, 100 per cent infection was obtained. It is evident that these oats are highly susceptible to this collection of smut.

On the other hand, the Red Rustproof type of *Avena sterilis* has proved to be entirely resistant. Six different strains, including Nortex, have been inoculated, and none of them has shown any infection. The varieties Burt, Nigra, and Selection, all recognized varieties of the Red Oat Group, have also proved to be negative to this collection.

The Hull-less oats, however, have proved to be susceptible, one strain giving 89.9 per cent infection. Liberty was tested in only one experiment, and gave a comparatively low number of infected plants. Orientalis (Seed No. 246) proved to be extremely resistant.

Among the *Sativa* types several, including Bicknell, Black Diamond, Canadian, Trisperma, Victor, and Winter Turf, gave high percentages of infection, and thus every indication of extreme susceptibility to this race. The variety Monarch gave 22 infected plants out of a total of 129 (17 per cent). Various other varieties, including Black Mesdag, Early Gothland, Green Russian, Joanette, Markton, Nebraska No. 21, Rosman, and Scottish Chief, proved highly resistant. No infected plants were obtained with *Avena strigosa* or *A. brevis*. On the other hand, *A. barbata* gave 100 per cent infection.

Two other collections have given results very similar to those just described. Collection No. 13 was obtained from Mr. T. R. Stanton, Office of Cereal Crops and Diseases, U. S. Department of Agriculture, who collected the smut on Fulghum oats at Lawton, Oklahoma, in June 1925; Collection No. 14 was obtained from Mr. P. B. Dunkle, Superintendent of Sub-Station No. 6, Texas Agricultural Experiment Station, Denton, Texas, also being collected on the variety Fulghum, in June 1925. In general, these two collections have given results corresponding with those obtained with No. 12. However, two or three differences stand out. While practically negative results were obtained with Collection No. 12 on *A. orientalis* (Seed No. 246), with Collection No. 13, 21 out of 45 plants (46.6 per cent) were infected, and with Collection No. 14, 11 out of 42 plants (26.1 per cent). Early Gothland gave negative results with No. 12, 96 plants being inoculated, and with No. 13, 29 plants out of 78 (37.1 per cent) were found infected, and with No. 14, 28 plants out of 72 (38.8 per cent). These results suggest the possibility of further specialization in these collec-

tions, although they all have the common capacity for attacking severely the Fulghum strains of Red oats.

Race X is based upon Collection No. 15. The original material was received from Mr. Dunkle in June 1925. It was collected on the Red Rustproof variety. Early experiments showed that

TABLE 5

Results with Ustilago Avenae (Pers.) Jens.

SPECIES AND VARIETY	SEED NO.	*Avenae* NO. 12 Tennessee			*Avenae* NO. 13 Oklahoma			*Avenae* NO. 14 Texas			*Avenae* NO. 15 Texas		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena barbata Brot.	830	16	16	100.0	15	15	100.0	18	18	100.0	16	12	75.0
Avena brevis Roth	289	43	0	0	38	0	0	29	0	0	18	0	0
Avena nuda L.													
Hull-less	30	109	98	89.9	83	46	55.4	94	56	58.5	59	0	0
Liberty	292	18	3	16.6	19	4	21.0	19	7	36.8	20	0	0
Avena orientalis Schreb.	246	59	1	1.6	45	21	46.6	42	11	26.1	37	0	0
Avena sativa L.													
Bicknell	341	38	34	89.4	39	12	30.7	37	31	83.7	15	1	6.6
Black Diamond	116	81	62	76.5	50	35	70.0	57	44	77.1	60	1	1.6
Black Mesdag	70	93	0	0	80	0	0	77	0	0	36	0	0
Canadian	119	84	80	95.2	55	50	90.9	58	44	75.8	58	49	84.4
Early Champion	150	—	—	—	—	—	—	—	—	—	18	0	0
Early Gothland	152	96	0	0	78	29	37.1	72	28	38.8	68	0	0
Green Russian	316	39	0	0	32	2	6.2	28	5	17.8	—	—	—
Joanette	187	20	0	0	19	0	0	18	0	0	20	0	0
Markton	752	35	0	0	37	0	0	34	0	0	42	0	0
Monarch	161	129	22	17.0	79	25	31.6	79	2	2.5	64	0	0
Nebraska No. 21	280	31	0	0	29	1	3.4	25	1	4.0	18	0	0
Rossman	322	30	0	0	28	3	10.7	30	1	3.3	—	—	—
Scottish Chief	124	72	2	2.7	58	6	10.3	50	3	6.0	38	0	0
Trisperma	64	27	16	59.2	25	2	8.0	26	8	30.7	17	0	0
Victor	126	94	75	79.7	58	27	46.5	56	30	53.5	35	2	5.7
Winter Turf	236	22	21	95.4	—	—	—	—	—	—	—	—	—
Avena sterilis L.													
Burt	175	89	1	1.1	62	4	6.4	66	2	3.0	32	3	9.3
Frazier	914	39	27	69.2	58	19	32.7	59	36	61.0	58	0	0
Fulghum	129	120	75	62.5	118	79	66.9	122	90	73.7	60	0	0
"	257	79	64	81.0	36	24	66.6	58	51	87.7	43	0	0
"	696	91	61	67.0	43	35	81.3	45	39	86.6	20	0	0
"	745	81	67	82.7	96	59	61.4	95	69	72.6	47	1	2.1
Kanota	264	89	71	79.7	82	48	58.5	81	68	83.8	15	0	0
"	906	38	27	71.0	54	30	55.5	54	42	77.7	38	1	2.6
Navarro	946	19	0	0	32	0	0	37	0	0	33	0	0
Nigra	130	37	0	0	36	0	0	34	0	0	37	2	5.4
Nortex	907	37	0	0	55	0	0	57	0	0	51	25	49.0
Red Rustproof	131	101	0	0	83	0	0	86	0	0	81	52	64.1
" "	263	18	0	0	19	0	0	13	0	0	49	28	57.1
" "	265	85	0	0	69	1	1.4	70	0	0	150	91	60.6
" "	355	90	0	0	69	0	0	57	0	0	36	27	75.0
" "	746	87	0	0	88	0	0	83	0	0	69	39	56.5
Selection	132	35	0	0	31	0	0	35	0	0	32	0	0
Avena strigosa Schreb.	587	20	0	0	20	0	0	20	0	0	—	—	—

the original material was a mixture, but a very distinct race, capable of attacking Red Rustproof, was separated out. Five strains of this variety gave infections ranging from 56.5 to 75.0 per cent. Nortex, in three tests, gave 25 infected plants out of 51 (49.0 per cent). In striking contrast to these results,

the Fulghum strains gave negative results. Burt, Navarro, and Selection also proved to be essentially negative.

This race also proved incapable of infecting *Avena brevis*, *A. nuda* and *A. orientalis*. It was not tested on *A. strigosa*. Among the varieties of *A. sativa*, only one, Canadian, showed any conspicuous susceptibility to the race. With this variety, 49 out of 58 infected plants (84.4 per cent) have been obtained. *Avena barbata* has proved to be highly susceptible in the one experiment in which it was inoculated.

Race XI is based upon Collection No. 3. This was made by Dr. C. R. Hursh at Bandole, France, in May 1924, on *Avena barbata*. It has proved to be a very distinct specialized race of the loose smut, being capable of infecting only *A. barbata*, the host upon which it was collected. Practically negative results have been obtained with *A. brevis*, *A. nuda*, *A. strigosa*, *A. sterilis*, and six varieties of *A. sativa*, including Black Mesdag, Canadian, Early Gothland, Monarch, Scottish Chief, and Victor.

The evidence is clear that at least eleven distinct races of loose smut are found among the collections which have been used in these experiments. It is further probable that one or two other races may be differentiated. Further experiments, however, will be necessary in order to determine this.

The outstanding features of all of these races may be mentioned. *Avena barbata* is susceptible to all of them, although it has not been tested with Races II and III. Extremely high infections have been obtained with such diverse races as I and IX.

In contrast to *Avena barbata*, *A. brevis* has proved to be entirely resistant. It has been tested with all of the different races, and not a single plant has been found to be infected. Only one strain of *A. strigosa* has been used with these races, and it has proved essentially negative in every case except with Race I. It is possible, of course, that other strains or varieties of *A. brevis* and *A. strigosa* would show a susceptibility to one or more of these specialized types.

Avena orientalis (Seed No. 246) has proved to be highly susceptible to only Race I. It is somewhat susceptible to Collections No. 13 and 14, and this may be sufficient to separate these collections off from No. 12, which are now grouped as

Race IX. Green Mountain is very susceptible to Races I, II, III and IV, but has proved to be negative to V, VI, VII, and VIII, not having been tested with the remaining three.

Hull-less (Seed No. 30) is very susceptible to Races I, II, III, IV, V, and IX, being negative to all the others. Liberty

TABLE 6

Summary of results with Ustilago levis (K. & S.) Magn.[a]

SPECIES AND VARIETY	SEED NO.	PHYSIOLOGIC RACE								
		I					II	III	IV	V
		Missouri	Canada	Washington	Holland	Italy	Wales	France	England	China
		COLLECTION NUMBER								
		1	7	8	9	4	6	3	5	10
Avena barbata Brot.	830	4	—	—	—	5	4	5	5	—
Avena brevis Roth	289	1	2	2	2	2	5	1	2	0
Avena nuda L.										
Hull-less	30	5	5	5	5	5	1	0	2	4
Liberty	292	5	5	5	5	5	—	0	0	4
Avena orientalis Schreb.	246	1	0	0	2	0	0	0	0	0
Green Mountain	110	5	5	5	5	5	—	0	0	0
Avena sativa L.										
Bicknell	341	1	1	1	1	1	0	1	1	0
Black Diamond	116	1	1	3	3	2	0	0	4	0
Black Mesdag	70	0	0	0	0	0	0	0	0	0
Black Norway	118	0	0	0	0	0	0	0	0	0
Canadian	119	5	5	5	5	5	1	5	5	5
Early Champion	150	5	5	5	5	5	0	0	0	0
Early Gothland	152	1	1	0	0	0	0	1	1	0
Green Russian	316	0	0	0	0	0	0	0	1	—
Joanette	187	0	0	0	0	0	—	5	4	0
Markton	752	1	0	0	0	1	0	0	0	0
Monarch	161	5	5	5	5	5	0	5	5	0
Monarch Selection	162	0	0	—	0	1	0	0	0	0
Nebraska No. 21	280	0	1	0	1	0	0	0	0	0
Rossman	322	0	0	1	0	2	0	0	0	—
Scottish Chief	124	0	0	0	0	0	0	0	0	0
Trisperma	64	0	0	0	0	0	0	0	1	0
Victor	126	5	5	5	5	5	0	4	5	5
Avena sterilis L.										
Burt	175	2	1	1	2	1	0	0	1	1
Fulghum	129	1	0	0	0	0	0	0	0	0
Navarro	946	0	0	—	0	—	—	—	0	—
Red Rustproof	131	1	0	0	0	0	0	0	0	0
Avena strigosa Schreb.	587	4	3	4	3	4	5	3	2	1

[a] In the body of this table numerals are used as symbols with the following significance:
— = No trial
0 = No infection
1 = 1–10 per cent
2 = 11–25 per cent
3 = 26–50 per cent
4 = 51–75 per cent
5 = 75–100 per cent

oats usually corresponded very closely with this variety.

Among the varieties of *Avena sativa*, Black Mesdag and Markton were completely resistant to all of the races; no infections were obtained with either of them. Markton was not

used in the experiments with Race XI. The variety Canadian has proved to be extremely susceptible. It was attacked by all of the races except XI. It is further interesting that it is the only variety of this group which was infected by the Red Rustproof Race. Victor is almost as susceptible a variety as Canadian. Its susceptibility corresponded with this variety in every respect, except that it proved to be resistant to Race X as well as to Race XI. The other thirteen varieties grown varied greatly in their susceptibility to the different races, and on this account made possible the differentiation between the different collections.

The varieties of *Avena sterilis* have proved resistant to all the races except two. The Fulghum types are very susceptible to Race IX and the Red Rustproof types to Race X. These races are distinguished respectively by their capacity to infect Fulghum and Red Rustproof oats.

It is further interesting to note that Miss Sampson (1929) has described a specialized race of *Ustilago Avenae* which is capable of attacking *Avena brevis*. The material was collected on *A. strigosa*, and the race is especially characterized by its capacity for infecting the three subspecies of *A. strigosa—pilosa*, *orcadensis*, and *glabrescens*—as well as *A. brevis*. It has proved to be entirely negative on *A. nuda* and varieties of *A. sativa*.

PHYSIOLOGIC RACES OF USTILAGO LEVIS

Nine different collections of the covered smut obtained from different sources have been used in more or less extended experiments. Practically the same series of species and varieties of oats have been used as those employed in the different series with the loose smut. The data are recorded in tables 6 to 9.

The outstanding features of all the nine collections are as follows:

First. The high degree of susceptibility of *Avena barbata* to all the collections with which it was inoculated. Unfortunately, it was not included in the series with four of the collections of covered smut. In all the other cases, high percentages of infection, ranging from 72 to 100 per cent, have been obtained.

Second. *Avena brevis* has usually been infected to a slight degree, only one collection giving negative results. With

Collection No. 6 it has given almost 100 per cent of infected plants.

Third. *Avena orientalis* (Seed No. 246) has proved almost completely resistant to all of the collections, only one stray plant out of a total of 116, inoculated with Collection No. 1, being smutted; a few smutted plants were also obtained with collection No. 9. Green Mountain has given 100 per cent infection with several of the collections and negative results with the remainder.

Fourth. In the *Sativa* Group, many varieties stand out as sharply resistant: Black Mesdag, Black Norway, Early Gothland, Green Russian, Markton, Monarch Selection, Nebraska No. 21, Rossman, Scottish Chief, and Trisperma. In some of these varieties, notably Early Gothland, an occasional smutted plant has been observed, but usually all the plants in the experiments have remained free. The other varieties grown in the experiments have shown susceptibility to some of the collections, but resistance to the others.

Fifth. The varieties of *Avena sterilis* have, as a rule, shown a high degree of resistance. No collection of the covered smut has shown a marked capacity for attacking any variety of this species.

Sixth. Only one strain of *Avena strigosa* has been used in the experiments with all of the different collections; usually it has proved to be very susceptible, although one collection gave practically negative results.

On the basis of the behavior of the different collections on the varieties grown, especially Hull-less, Green Mountain, Bicknell, Black Diamond, Canadian, Early Champion, Joanette, Monarch, and Victor, at least five distinct races of the covered smut can be distinguished.

Race I is based upon Collection No. 1. The original material was collected near Columbia, Missouri, many years ago, and has been used in various experiments during the intervening years. Its outstanding features are its ability to severely infect Hull-less and Liberty, Green Mountain, Canadian, Early Champion, Monarch, and Victor. All of these have proved to be highly susceptible to this race of smut.

Avena brevis has generally given negative results, but occasionally partially smutted plants have been secured. These

are characterized by a marked dwarfing of the infected stalks as compared with the usual height of the normal.

The varieties Burt, Fulghum, and Red Rustproof have all shown a high degree of resistance. Occasionally an infected plant has been observed, particularly in the Burt and Fulghum varieties.

The strain of *Avena strigosa* has shown a high degree of susceptibility. Several other varieties belonging to the various

TABLE 7

Results with Ustilago levis (K. & S.) Magn.

SPECIES AND VARIETY	SEED NO.	*Levis* NO. 1 Missouri			*Levis* NO. 6 Wales			*Levis* NO. 10 China		
		No. pl.	No. inf.	% inf.	No pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena barbata Brot.	830	36	26	72.2	23	17	73.9	—	—	—
Avena brevis Roth.	289	103	9	8.7	112	109	97.3	35	0	0
Avena nuda L.										
Hull-less	30	118	112	94.0	127	2	1.5	55	35	63.6
Liberty	292	20	20	100.0	—	—	—	21	12	57.1
Avena orientalis Schreb.	246	116	1	0.8	51	0	0	36	0	0
Green Mountain	110	13	13	100.0	—	—	—	35	0	0
Avena sativa L.										
Bicknell	341	83	4	4.8	32	0	0	16	0	0
Black Diamond	116	53	5	9.2	15	0	0	33	0	0
Black Mesdag	70	100	0	0	75	0	0	38	0	0
Black Norway	118	57	0	0	28	0	0	19	0	0
Canadian	119	125	125	100.0	98	5	5.1	18	18	100.0
Early Champion	150	43	41	95.3	20	0	0	37	0	0
Early Gothland	152	135	5	3.7	87	0	0	20	0	0
Green Russian	316	73	0	0	62	0	0	—	—	—
Joanette	187	93	0	0	—	—	—	39	0	0
Markton	752	45	2	4.4	39	0	0	32	0	0
Monarch	161	160	157	98.1	106	0	0	55	0	0
Monarch Selection	162	47	0	0	25	0	0	40	0	0
Nebraska No. 21	280	40	0	0	5	0	0	17	0	0
Rossman	322	65	0	0	20	0	0	—	—	—
Scottish Chief	124	110	0	0	81	0	0	37	0	0
Trisperma	64	69	0	0	37	0	0	15	0	0
Victor	126	139	136	97.8	122	0	0	39	32	82.0
Avena sterilis L.										
Burt	175	52	6	11.5	44	0	0	29	2	6.8
Fulghum	129	86	4	4.6	64	0	0	20	0	0
Navarro	946	13	0	0	—	—	—	—	—	—
Red Rustproof	131	77	2	2.5	44	0	0	35	0	0
Avena strigosa Schreb.	587	90	63	70.0	82	79	96.3	48	2	4.1

subspecies of *A. strigosa* have also proved to be very susceptible. Individual tests have been made with *pilosa*, *orcadensis*, and *glabrescens*. One strain, however, has given negative results.

Four other collections have given practically the same results as those obtained with Collection No. 1: No. 4 collected by Dr. C. R. Hursh near Bologna, Italy, in 1924; No. 7 by Prof. W. P. Fraser in Canada; No. 8 by Prof. George L.

Zundel at Pullman, Washington, and No. 9 by Dr. Theo. Roemer, who obtained it from Holland. These four collections from widely separated localities have run quite parallel to the original collection from Missouri. The varieties used in the present experiment have not been sufficient for showing any specialization of these collections, if such specialization actually exists.

Race II is based on material originally received from Miss Sampson in Wales in 1923, and data obtained from experiments with this collection have already been published. A second collection was received in 1925 from Dr. Pethybridge, who, however, obtained the material from Miss Sampson. The data presented in the table were secured with this collection, No. 6, but it has shown complete conformity with the original one received from Wales.

The conspicuous features of Race II are its capacity to infect *Avena brevis* and *A. strigosa*. Usually, 100 per cent of infected plants is obtained. It is equally severe on practically all varieties of *A. strigosa*, although one or two distinct strains have shown complete resistance; several strains of *A. brevis* have also proved to be entirely resistant. On the other hand, it is negative or nearly so on all varieties of *A. nuda*, *A. sativa*, *A. orientalis* and *A. sterilis*.

Race III is based upon Collection No. 3. The material was sent to me by Dr. C. R. Hursh from St. Cannot, France in 1924. The race shows a limited capacity for infecting oat varieties. It is entirely negative on the *Avena nuda*, *A. orientalis*, and *A. sterilis* groups, and only four varieties of *A. sativa* have proved to be susceptible, namely, Canadian, Joanette, Monarch, and Victor. It has not given very high prercentages of infection of *A. strigosa*, and only a few partially infected plants of *A. brevis* have been obtained.

The outstanding features of the race, as compared with I, are its inability to infect Hull-less, Liberty, Green Mountain, and Early Champion. It is equally conspicuous by its capacity for infecting Joanette, a variety which has given negative results with Race I.

Race IV is based upon Collection No. 5, which was sent to me by Dr. Pethybridge from Shinfield, Berkshire, England. It shows a close similarity to Race III. It has almost the same

ability to infect the varieties. It is negative or practically so on the Hull-less oats, Green Mountain, and Early Champion. It severely infects such varieties as Canadian, Joanette, Monarch, and Victor. It is distinguished from the previous race by its ability to infect Black Diamond. With this variety, out of 52 plants inoculated, 38 (73.0 per cent) have been smutted. On the other hand, 50 inoculated plants with Race III gave entirely negative results.

TABLE 8

Results with Ustilago levis (K. & S.) Magn.

SPECIES AND VARIETIES	SEED NO.	*Levis* NO. 7 Canada			*Levis* NO. 8 Washington			*Levis* NO. 9 Holland		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena barbata Brot.	830	—	—	—	—	—	—	—	—	—
Avena brevis Roth	289	68	11	16.1	47	9	19.1	72	9	12.4
Avena nuda L.										
Hull-less	30	75	61	81.3	56	46	82.1	83	71	85.5
Liberty	292	19	17	89.4	20	17	85.0	20	19	95.0
Avena orientalis Schreb.	246	43	0	0	52	0	0	51	6	11.7
Green Mountain	110	34	34	100.0	14	13	92.8	34	34	100.0
Avena sativa L.										
Bicknell	341	37	1	2.7	30	1	3.3	38	3	7.8
Black Diamond	116	31	3	9.6	16	7	43.7	32	12	37.5
Black Mesdag	70	51	0	0	52	0	0	54	0	0
Black Norway	118	19	0	0	17	0	0	17	0	0
Canadian	119	76	76	100.0	51	51	100.0	79	78	98.7
Early Champion	150	61	58	95.0	17	15	88.2	57	50	87.7
Early Gothland	152	61	1	1.6	52	0	0	60	0	0
Green Russian	316	15	0	0	10	0	0	15	0	0
Joanette	187	58	0	0	17	0	0	56	0	0
Markton	752	48	0	0	39	0	0	39	0	0
Monarch	161	120	113	94.1	54	54	100.0	119	110	92.4
Monarch Selection	162	19	0	0	—	—	—	20	0	0
Nebraska No. 21	280	32	3	9.3	24	0	0	29	1	3.4
Rossman	322	15	0	0	14	1	7.1	15	0	0
Scottish Chief	124	45	0	0	50	0	0	54	0	0
Trisperma	64	20	0	0	19	0	0	27	0	0
Victor	126	78	75	96.1	50	50	100.0	84	81	96.4
Avena sterilis L.										
Burt	175	41	4	9.7	36	3	8.3	46	8	17.3
Fulghum	129	39	0	0	37	0	0	38	0	0
Navarro	946	12	0	0	—	—	—	11	0	0
Red Rustproof	131	18	0	0	18	0	0	23	0	0
Avena strigosa Schreb.	587	83	22	26.5	31	19	61.2	83	25	30.1

Race V is based upon Collection No. 10. The original material came from the Experimental Farms at Sui-Yuan, Inner Mongolia, being sent to me by Prof. Chunjen C. Chen in 1927. The race stands out sharply by its ability to infect Hull-less and Liberty and also Canadian and Victor. It has proved to be negative or practically so to all the other varieties on which it has been tried. It is especially striking that it has failed to infect *Avena brevis*, *A. strigosa*, and such varieties of *A. sativa*

as Early Champion and Monarch. Unfortunately, it has not been used on *A. barbata*.

Miss Sampson (1929) has recently described a distinct new race of covered smut. She obtained a collection from England which proved capable of infecting severely certain varieties of *Avena sativa*, but was entirely negative on *A. strigosa orcadensis*, *A. brevis*, and practically so on *A. nuda*. It is evidently very close in its behavior to my Race IV.

TABLE 9

Results with Ustilago levis (K. & S.) Magn.

SPECIES AND VARIETY	SEED NO.	*Levis* NO. 4 Italy			*Levis* NO. 3 France			*Levis* NO. 5 England		
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena barbata Brot.	830	12	12	100.0	13	13	100.0	18	18	100.0
Avena brevis Roth	289	114	15	13.1	122	8	6.5	115	13	11.3
Avena nuda L.										
Hull-less	30	112	106	94.6	139	0	0	127	20	15.7
Liberty	292	17	15	88.8	18	0	0	17	0	0
Avena orientalis Schreb.	246	52	0	0	75	0	0	60	0	0
Green Mountain	110	34	34	100.0	39	0	0	37	0	0
Avena sativa L.										
Bicknell	341	29	2	6.8	25	1	4.0	27	1	3.7
Black Diamond	116	34	5	14.7	50	0	0	52	38	73.0
Black Mesdag	70	73	0	0	88	0	0	88	0	0
Black Norway	118	36	0	0	41	0	0	44	0	0
Canadian	119	97	97	100.0	106	105	99.0	145	138	95.1
Early Champion	150	36	34	94.4	38	0	0	62	0	0
Early Gothland	152	87	0	0	106	1	0.9	102	1	0.9
Green Russian	316	33	0	0	56	0	0	51	1	1.9
Joanette	187	37	0	0	36	31	86.1	55	29	50.9
Markton	752	50	2	4.0	45	0	0	37	0	0
Monarch	161	123	119	96.7	136	125	91.9	195	162	83.0
Monarch Selection	162	43	1	2.3	40	0	0	45	0	0
Nebraska No. 21	280	27	0	0	27	0	0	14	0	0
Rossman	322	19	2	10.5	20	0	0	15	0	0
Scottish Chief	124	68	0	0	99	0	0	84	0	0
Trisperma	64	50	0	0	50	0	0	44	1	2.2
Victor	126	90	88	97.7	120	77	64.1	148	125	84.4
Avena sterilis L.										
Burt	175	38	3	7.8	56	0	0	86	2	2.3
Fulghum	129	59	0	0	75	0	0	72	0	0
Navarro	946	—	—	—	—	—	—	10	0	0
Red Rustproof	131	28	0	0	34	0	0	39	0	0
Avena strigosa Schreb.	587	105	70	66.6	109	32	29.3	122	20	16.3

DISCUSSION

In the present experiments, fifteen different collections of *Ustilago Avenae* and nine of *U. levis* from widely separated localities have been studied with reference to their behavior on twenty-eight varieties and strains of oats belonging to seven different species. As a result of these experiments, eleven specialized races of loose smut and five races of covered smut have been differentiated on the basis of their capacity for infecting the varieties of oats grown.

So far as tested, all of the collections have proved capable of infecting *Avena barbata*. This species has been particularly susceptible to all races with which it has been inoculated. It is especially interesting that one race of *Ustilago Avenae* is distinguished by the fact that it is capable of attacking only this species.

None of the races of loose smut have shown any capacity for attacking *Avena brevis*. On the other hand, all the races of covered smut are capable of infecting this species, with the exception of Race V. However, only one race, II, has been able to produce a severe infection on this oat. In the other cases, relatively few plants have been smutted, and these only partially so.

Only two varieties of *Avena sativa*, Black Mesdag and Markton, have shown a conspicuous resistance to all races of both loose and covered smut. On the other hand, the varieties Canadian and Victor have shown unusual susceptibility to the various races of both species of smut. There are, however, two or three races to which these varieties have proved to be resistant.

The other varieties of *Avena sativa*, together with those of *A. nuda*, *A. orientalis*, *A. sterilis*, and *A. strigosa*, have shown varying degrees of susceptibility to the races of loose and covered smut, and it is through their behavior that the different races have been differentiated. It is particularly noteworthy that Black Norway, Early Gothland, Green Russian, Nebraska No. 21, Rossman, Scottish Chief, and Trisperma are unusually resistant to all races of covered smut, while extremely susceptible to one or more distinct races of loose smut. On the other hand, Monarch, and to some extent, Joanette, have proved more susceptible to the covered smut races.

It is interesting to note that there are sharply defined races of loose smut capable of attacking varieties of *Avena sterilis*, one being peculiar in its capacity for infecting Fulghum and another for infecting Red Rustproof. Further, I have found no well defined race of *Ustilago levis* which severely attacks any variety of this species. An occasional infected plant with some races of covered smut is observed, but so far, no distinct race of this smut, more or less restricted to these varieties, has been discovered.

It must be emphasized that the data obtained are based upon the use of well defined strains of oats. Other selections passing under similar names may give entirely different results; for example, certain varieties and strains of both *Avena strigosa* and *A. brevis* differ strikingly from those used. Further, I have a selection of Monarch which is exactly the reverse in its behavior to the one which I have grown in these experiments. It is negative to Race I of the covered smut, while highly susceptible to Race I of the loose smut.

It is obvious that these specialized races have special significance in the problem of the study of inheritance of smut resistance. It is just as important, in such investigations, to use known races of smut as it is pure line material of the oat varieties.

BROOKLYN BOTANIC GARDEN
BROOKLYN, N. Y.

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A morphologic study of the variations in Stellaria aquatica with special reference to symmetry and sterility

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(WITH THIRTY-TWO TEXT FIGURES)

The variability within the genus *Stellaria*, and even within certain species of that genus, has long been known and strongly emphasized; the coherence or trends within the genus and species, however, are by no means agreed upon, though the flowers form a very wide-ranging and possibly evolutionary series.

In the present study particular attention has been paid to *Stellaria aquatica* (L.) Scop. and *Stellaria media* (L.) Cyr., not with a view to distinguishing new varieties, but rather with the aim of determining the biological type for each of these species, which vary strikingly, not merely in different individuals, but, especially in *S. media*, in different parts of the same plant. The present paper gives the data on *S. aquatica*, and is to be followed by a study of the floral types in *S. media*, and of the correlation of external and internal variations in the flowers of these two species.

S. aquatica represents the maximum development, particularly as regards the number of parts in the flower, not only for the members of the genus, but for the Caryophyllaceae in general; and from such a type the increasing reduction in the number of parts in the flower of the Alsinoideae may well have progressed.

LITERATURE REVIEW

Linnaeus (in the *Species Plantarum*, 1753), classifying plants on the basis of the number of stamens and carpels, recognized the genera *Alsine* (p. 272), in which he included *A. media*, with five stamens and three carpels; *Stellaria* (p. 421) with ten stamens and three carpels; and *Cerastium* (p. 437) with ten stamens and five carpels. Because of its ten stamens and five carpels he placed the species now recognized as *Stellaria aquatica* in the genus *Cerastium*. Thus began the confusion in the nomenclature of the genus *Stellaria* which has resulted in the following extensive list of the more important synonyms of this species.

Cerastium aquaticum Linnaeus, Species Plantarum 439. 1753.
Stellaria aquatica Scopoli, Flora Carniolica ed. 2. **1**: 319. 1772.
Alsine uliginosa Villars, Prospectus . . . . Dauphin. 48. 1779.
Cerastium maximum Gilibert, Flora Lithuanica **2**: 158. 1781.
Myosoton aquaticum Moench, Methodus plantas describendi 225. 1794.
Myosanthus aquaticus Desvaux, Jour. de Bot. Desv. II. **3**: 227. [1816?]. (See note on page 531.)
Malachia aquatica Fries, Flora Hallandica 77. 1817.
Larbrea aquatica Seringe in DeCandolle, Prodromus Syst. Nat. 395. 1824. Not *L. aquatica* A. St. Hilaire, Mém. Mus. Hist. Nat. **2**: 287. 1815. [=*Stellaria uliginosa* Murray, Prodr. Stirp. Gott. 55. 1770].
Cerastium deflexum DeCandolle, Prodromus Syst. Nat. 417. 1824.
Malachium aquaticum Fries, Novitiae Florae Suecicae 121–122. 1828; Hegi, Illustrierte Flora Mittel-Europa **3**: 348. 1911–1913.
Stellaria pentagyna Gaudin, Flora Helvetica **3**: 179. 1828.
Stellaria media α *aquatica* O. Kuntze, Revisio Gen. Plant. **1**: 52–55. 1891.
Alsine aquatica Britton, Mem. Torrey Club **5**: 356. 1894; Small, Flora S. E. United States 421–423. 1913; Rydberg, Flora Rocky Mountains 268–271. 1917.

It is interesting to observe that the first change from the Linnaean disposition of the species was in its transference by Scopoli in 1772 from *Cerastium* to *Stellaria*, a position which would doubtless be regarded by a majority of modern taxonomists as expressing its natural affinity, and which appears to be confirmed by the present investigation. It will be seen, however, from the list, that opinion has varied widely in regard to the disposition of *S. aquatica*, from the attempts to constitute a separate genus for it on the one hand, to Kuntze's reduction of it to a mere variety of *S. media* on the other. The generic name *Malachium* Fries had rather wide acceptance in the literature of continental Europe during the nineteenth century (and even down to Hegi's recent *Flora*), though *Myosoton* Moench clearly has priority. Britton, finally, has revived the ancient genus *Alsine* (based according to him on the type species *A. media* L.), and restored to it the species separated under *Stellaria* by Linnaeus; in this he has been followed by Small, Rydberg, and some other American authors.[1] In Europe the

[1] Further confusion in regard to the use of *Alsine* has been introduced by the fact that House, in his *Annotated list of the ferns and flowering plants of New York State* (N. Y. State Mus. Bull. 254: 321–322), has interpreted the Linnaean genus *Alsine* as synonymous with *Spergularia* Pers. and *Tissa* and *Buda* Adans., while with Pax (1889) in Engler and Prantl, and other European authors the genus *Alsine* Wahlenb. has been in use for an entirely different group of species.

name *Stellaria* has been largely retained (Pax, 1889, in Engler and Prantl; Index Kewensis, 1895; Richter, 1897; Béguinot, 1910; Engler and Gilg, Syllabus der Planzenfamilien, ed. 9–10, 1924). *Stellaria* is used also in *Gray's New Manual of Botany*, ed. 7, and by some other American botanists.

When the species *S. aquatica* is included in the genus *Stellaria*, the more primitive character of its pistil is commonly emphasized by making it the sole species in a section of the genus, as in the section Malachium of Hooker (Flora British India 1: 229–230. 1875), or the subgenus Myosoton of Pax (1889).

A number of varieties of *S. aquatica* have been described. Lejeune[2] in addition to *Cerastium aquaticum* described *C. scandens*, which he said differed from the former by its twining habit. Fries[3] mentioned a variety, *Malachium aquaticum β saxatile* with the stems four-angled, the leaves narrower than in the typical form, and the peduncles few and terminal. Fries recognized the possible influence of environment in this case, and added in a note that this form growing among the rocks of a canal would be exposed to heat and strong light. In his general description of *S. aquatica* Petermann[4] characterized it as having a stem smooth below, glandulose-pubescent above, and then distinguished two forms, the first with the stem pubescent, the second with the stem smooth, but with the 'corymb only glandulose-pubescent.' Willkomm[5] noted a form which he designated *Malachium calycinum*, differing from the normal form in its single line of cauline hairs, shorter leaves, non-glandular pedicels and calyx, and especially in the short, included petals. Godron[6] described two varieties for Lorraine, *M. aquaticum α scandens*, 6–8 dm., climbing, leaves of the floral stem all sessile; and *M. aquaticum β arenarium*, a smaller plant, 1–3 dm., less developed in all its parts, with the lower leaves of the fertile stems petioled, truncate at the base, and the inflorescence poorly developed. The variety *β arenarium* was found in sand. Schur[7] described two varieties: *M. aquaticum a alpinum*, with stems prostrate, 2.3–3 dm. long, leaves and stem pubescent, the lower leaves petioled; and *M. aquaticum b angustatum* hav-

[2] Lejeune, Flore des environs de Spa 210–211. 1811. [3] Fries, Nov. Fl. Suec. 121–122. 1828. [4] Petermann, Flora Lipsiensis 330–331. 1838. [5] Willkomm, Spicilegium florae Hispanicae. Bot. Zeit. **5**: 233–241. 1847. [6] Godron,

ing stems erect-ascending, hirsute but smooth above ('superne glabris') the leaves 2.5 cm. long, 12.5 mm. wide, and purple veined. In a later publication Schur[8] described three additional varieties: *M. aquaticum arenosum glomeratum*, distinguished chiefly by the bushy, stiff, upright character of the plants, the leaves smooth or nearly so, and the flowers fascicled at the apex of the stem; this form was found in sandy places and along railroad tracks; *M. aquaticum silvaticum molle*, characterized by its soft, dark green, much branched habit, glandular hairy above, leaves sharply punctate with white spots; flowers somewhat smaller than in the normal form; and *M. aquaticum hungaricum*, having recurved styles, plants slightly hairy and glandular, leaves all stalked.

The stem and inflorescence of the Caryophyllaceae, in addition to the treatment afforded them in the manuals, are discussed in a general way by Eichler (1878), Pax (1889), and Warming (1904) . For *Silene* these features were taken up by Godron (1847) and Rohrbach (1868). The branching and inflorescence of the Caryophyllaceae were described more critically in the older literature by Wydler (1843, 1844, 1847, 1851, 1859), and by Wichura (1844, 1846, 1847). Wydler (1859) gave the general characters of the branching in *S. media* and *S. aquatica*, and Béguinot (1920) in *S. media*. Wydler made a few errors which were pointed out by Wichura and which he later acknowledged. The results given below are in general agreement with theirs, though the point of approach is somewhat different.

The arrangement of the branches is of course intimately associated with the arrangement of the leaves on the stem; and the subject of phyllotaxis is by no means settled. For many years the Fibonacci series, emphasized by Schimper and by Braun (1835) and others has served for textbook treatment of the subject. The contact, pressure and displacement (or slipping) theory as the explanation of leaf relationships was put forth by Schwendener (1878, 1901) and supported among others by Weisse (1889). It was extended and modified by Van

Flore de Lorraine, ed. 2. **1**: 126–127. 1857. [7] Schur, Enum. Plant. Transsilvaniae 115–116. 1866. [8] Schur, Verh. Naturf. Ver. Brünn **15**[2]: 142–143. 1877.

Iterson (1907). However in its original form this theory is not generally accepted. It has been severely criticized among others by Winkler (1901, 1903), who showed that in some plants at least the 'contact' theory is impossible, and by Church (1901a, b, 1902, 1904, 1920). Emphasizing the study of the shoot apex in phyllotaxis, Church refers the phyllotax-mechanism to 'an initial choice of curve systems, comparable with the isolation of equal-spaced lines of growth-potential'; furthermore every lateral primordium he conceives as originating as 'a centric disturbance in a centric growth system.' He strongly criticizes the validity of the exact fractional divergences expressed by the numbers of the Fibonacci series, especially at the primordial apex. Church's work has been extensive and has been emphasized by Jaeger (1917) and Crow (1928).

It is well known that in some of the lower plants, as in some of the mosses and liverworts, there is a close relationship between the growth of the apical cell and the arrangement and size of the leaves. Even there, however, disturbing influences such as apical torsion must be considered (Correns, 1899). But the literature on the course of the cell divisions in the Spermatophyta is by no means as illuminating. The researches of Hanstein (1868), Strasburger (1872), Schwendener (1879), Groom (1885), and Koch (1891) satisfactorily disproved the contention of a general occurrence of single apical cells in the shoots of the Spermatophyta advocated by Dingler (1882, 1886) and Korschelt (1884), and correlations between apical cell divisions and leaf arrangements established in the lower plants can thus not be directly extended to the seed plants (see also Schwendener, 1885). The rules of rectangular intersection and division into equal parts formulated by Sachs (1878, 1887) as applied to cell divisions are not very helpful in the study of the relationship between the growth of the shoot and leaf arrangement, and the correlation between cell divisions in the shoot apex and phyllotaxis is left unanswered.

According to the view advocated especially by Velenovský (1887, 1907) and Čelakovský (1901, 1902) the plant is composed of a number of units ('Glieder'). Each unit has been variously called a 'phyton' (Gaudichaud, 1841), 'anaphyton' or 'anaphytum' (Schultz-Schultzenstein, 1843, 1847), and 'filopodio'

(Delpino; 1883). According to this theory each limb or unit is derived from the preceding by lateral growth, and the terminal growing point of the stem is of secondary origin. This view is based especially on embryological and seedling evidence. According to Velenovský a unit (anaphyt) consists of an internode and the node next above it, whether that node has one, two or several leaves. Čelakovský maintains on the other hand that this is only true in certain stems, such as those of the grasses; there a 'Sprossglied' consists of an internode and the node with its leaf next above it. However in stems having the usual spiral or whorled arrangements, in which a leaf subtends merely a portion of the stem, an anaphyt consists of a sector of the stem between one leaf and the next which stands directly above it, and the upper of these two leaves. Thus in the spiral arrangement the stem is composed of a number of 'Stengelglieder' arranged side by side, but beginning and terminating at different levels. According to both of these views the opposite leaf arrangement is of secondary origin. Church too refers to it as an 'afterthought.'

The occurrence of antidromy in plants has long been known, having been repeatedly discussed by Wydler and Wichura. Macloskie (1895 a, b, c, 1896 a, b, c) thought at first that plants were essentially internally homodromic, but antidromic as regards different individuals of the same species; he gave a list of plants to illustrate this, and even suggested the possible genetic significance of this phenomenon. However he later found that the principle of homodromy within the individual, antidromy between different individuals was not constant, and concluded that the law of antidromy was more complex than he had at first anticipated.

The external similarity between the clockwise and counterclockwise arrangement of leaves or branches on an axis and the spirals of the shells of gasteropods is rather suggestive. As shown by Crampton (1894), Holmes (1900), Conklin (1903), and others the dextral and sinistral spirals are correlated with a definite spiral cleavage pattern; no such relationship has been reported in the seed plants. The production of leaf primordia in a definite pattern on the stem apex is different in some respects at least from the continuous spirals of gasteropod

shells. The similarities in principle, especially from the mathematical point of view, between phyllotaxis and shell construction in some of the Foraminifera are discussed by Van Iterson (1907). He also points out certain differences: on the vegetative apex the new leaves are established on the inner side of the folioidal system, while new chambers in the shells of the Foraminifera are laid down on the outside; the constant factors are different and there are other dissimilarities.

The variability within the flowers of the genus *Stellaria* has come to be almost proverbial; it is discussed or mentioned in many of the textbooks. Among the more detailed studies of the different kinds of flowers should be mentioned first the very extensive researches of Béguinot (1910, 1920, 1921) as well as those of Reinöhl (1903) and Burkill (1895). These have been concerned especially with *S. media*, which displays the greatest variability of any of the members of the genus. Béguinot studied many of the varieties of that species. *S. aquatica* has been investigated by Béguinot (1914), who found the styles varying in number from six to two, and Kuntze (1891) who also reported on the variations in the gynoecium. Bentham (1861, 1862) found the styles in Indian specimens not infrequently reduced to three; interesting additional evidence is also offered by many of the descriptive floras, some of which are listed above.

In the mature flower of *S. aquatica* the stamens opposite the sepals appear to be inside of those opposite the petals. This arrangement is the reverse of that found in most flowers and has given rise to the disputed question of the real nature of obdiplostemony. This was debated in the older literature which is reviewed by Eichler (1875). Hofmeister (1868) considered the stamens opposite the sepals as the original whorl; those opposite the petals he considered to have developed later and become interpolated between the whorl of petals and sepal stamens. Eichler at first adopted the view previously advocated by A. St. Hilaire that the stamens opposite the petals are merely split off from the petals and hence are really part of that whorl, the stamens opposite the sepals being the true whorl. Lüders (1907) and Wettstein (1911), on the other hand, consider the petals in the Caryophyllaceae to have arisen from the sta-

minal whorl. Later, however, Eichler (1878) accepted the theory suggested by Payer (1857) and advocated especially by Čelakovský (1875) that the diplostemonous arrangement was the original one, but that by displacement ('Verschiebung') the whorls became reversed as to position. This view is also accepted by Velenovský (1910). However, Čelakovský (1894) later abandoned this view and considered the obdiplostemonous arrangement associated with reduction. Schumann (1889) pointed out that obdiplostemony may be found in flowers in which the stamens opposite the sepals are the first to develop, and in others in which those opposite the petals develop first; he suggested contact as an explanation of the position of the carpels with reference to the two staminal whorls.

Payer (1857) figured the stages in the development of the flower of *S. aquatica*, and as shown in his figures 6 and 7, plate 73, the first stamens arise alternating with the petals. In figures 10 and 17, plate 73, he drew the sepal stamens higher up on the axis than the petal stamens. Schumann (1889) stated that in *Melandrium* and *Lychnis* the episepalous stamens originate first and lower down on the axis. *Malachium aquaticum*, he reported, differs in that the epipetalous stamens are inserted deeper than in *Melandrium*, but he was unable to determine whether or not the two whorls were inserted at the same level. Rendle (1925) states that the antesepalous stamens in the Caryophyllaceae not only arise before the antepetalous, but that their vascular strands in the floral axis stand outside of those leading to the antepetalous stamens, and that the obdiplostemony is therefore only apparent.

In may be worth while, furthermore, to call attention to the fact that, although in most families characterized by obdiplostemony (*e.g.* Crassulaceae, Geraniaceae, Onagraceae, and Ericaceae) the phenomenon finds complete expression, that is, in association with the reversed position of the two stamen whorls the carpels also are placed opposite the petals (rather than opposite the sepals), in the Caryophyllaceae, on the other hand, as shown by Eichler, two degrees of obdiplostemony are exhibited: an incomplete obdiplostemony in *Cerastium* (as also in *Lychnis* and *Viscaria* of the Silenoideae, cf. Eichler's diagram, 1875, p. 106), where only the two whorls of anthers

show the reversed position, the carpels still being opposite the sepals; and apparently complete obdiplostemony in *Stellaria aquatica* (as also in *Spergula arvensis* L.), where the carpels are opposite the petals.[9] *Cerastium*, then, may be regarded as the most primitive genus we have in the Alsinoideae.

Both the stamens and pistils of *S. aquatica* show sterility to some extent. In the case of the androecium at least, in plants growing wild, this is a seasonal and hence in a measure a cyclic phenomenon. Sterilities associated with the partial or complete abortion of one or the other or both kinds of sporophylls are rather general in the Spermatophyta. Thus for example Stout (1922) found flower abortion at the beginning of the flowering period in *Brassica pekinensis* and *Brassica chinensis*, and arrested development of the flowers at the end; in addition he found other classes of sterility in the intervening period. The modification of one or more of the stamens into staminodia in the Caryophyllaceae was discussed by Darwin (1868, 1877). It is treated further by Henslow (1888) and Rendle (1925), both of whom contend that low temperature is the cause.

Among the classifications of sterility may be mentioned that of Stout (1916) in which he distinguishes three main groups: sterility from impotence, sterility from incompatibility, and embryo abortion. In the first of these, which includes the kinds of sterilities described below for *S. aquatica*, Stout mentions complete impotence involving either the absence of all floral and sex organs, or the lack of sporophylls only, and partial or com-

[9] This difference of carpel position seems to furnish a more fundamental basis for the separation of the genera *Cerastium* and *Stellaria* than that usully given in our current manuals, viz. the form and dehiscence of the capsule. It is surprising that this difference has been overlooked by the authors of '*Gray's New Manual of Botany*', 7th Edition, for in spite of their general adherence to the taxonomic arrangement of Pax (1889), who treated this point correctly, they have made the erroneous and misleading statement in both key and generic diagnosis that the styles of *Stellaria* are opposite the sepals. That not only styles (as shown in the figures illustrating this paper) but also the entire carpels are opposite the petals may easily be demonstrated in transverse sections of young flower buds, where the ovary shows complete septa opposite the sepals, which break down to produce the 'free central placenta' of the mature pistil. Even when the carpels are reduced to three (as in *S. media*, cf. Eichler's fig. 41, F) two of them are essentially opposite petals. —T. E. H.

plete impotence with reference to one or the other or both types of sporophylls. Sirks (1917) distinguishes two main classes of sterility: sterility of the gametes, and sterility of the zygotes; the former he subdivided into partial unilateral, partial bilateral, total unilateral and total bilateral sterility of the gametes. The sterilities in *S. aquatica* discussed below can also be relegated to these different categories.

DISCUSSION OF SYSTEMATIC LITERATURE AND DESCRIPTION

Whether the different forms of *S. aquatica* which have been described, that amount to different varieties, will stand the test of being grown and propagated from seed is very problematical indeed. Whether the twining habit is a characteristic peculiar to one or more varieties, or whether it depends upon the presence and character of other neighboring plants has not been investigated. The stems of *S. aquatica* are usually more or less four-angled, and Fries was aware of the possibility of environmental influences in the characteristics of the variety *β saxatile*. Petermann's distinction, one variety having only the 'corymb' glandulose-pubescent, the other having the upper part of the stem pubescent as well, also needs further investigation. In the plants found in the vicinity of the city of New York it is not unusual to have just a single internode, directly below the inflorenscence, glandulose-pubescent; in other cases several internodes just below the inflorescence are glandulose-pubescent. If Petermann had a form constantly glabrous up to the first flowering node it would certainly deserve to be ranked as a distinct variety; on the other hand in a fluctuating character like this, extended study is necessary before forms differing in the extent of pubescence can be admitted as good varieties. Ricker (1916) showed that the leaves of *Castanea mollissima* when exposed to strong light are densely pubescent with stellate and jointed hairs, while shaded leaves on the same tree are practically glabrous, all intergradations between these two types existing on the same individual. On the other hand the extensive researches of Béguinot (1907, 1910, 1920, 1921) on *Stellaria media* indicate that the extent of hairiness is a feasible line of approach to the separation of new varieties. Willkomm's description also suggests that he was dealing with a distinct variety. However the lowest pubescent internode not

uncommonly has just a sparse line of hairs, instead of being hairy throughout; sometimes this single line of hairs only extends part way down the internode. As for the short petals, it is not at all unusual for plants of *S. aquatica* to have some flowers with the petals equal to or shorter than the calyx, and in the colder weather of November the majority of the flowers in the vicinity of the city of New York are of this character. Willkomm's observations were apparently based on a limited amount of herbarium material, so much so that he was unable to report on the character of the lower leaves and the roots; here again, although the description is very suggestive, further research, especially on living growing plants, is necessary before the variety can be considered established. The two varieties of Godron may well be distinct. But the size of the plants is beyond doubt partly subject to the environment; and the plants, rooting at the nodes and dying off in the older parts may lose many of their stalked leaves. The two varieties of Godron are apparently different and should be further sought and studied. Of Schur's forms, the *M. aquaticum a alpinum* is similar to the *M. aquaticum β arenarium* of Godron. The form *M. aquaticum b angustatum* of Schur, with its purple veins and stem hirsute, smooth above—just the reverse of the condition usually obtaining—is striking indeed; the white punctate character of the leaves of the variety *M. aquaticum silvaticum molle* is very unusual; and the 'zurückgerollte Griffel' of the variety *M. aquaticum hungaricum*, in flowers that have been open for some time are the normal thing; if the styles are recurved when the flowers first open it is a noteworthy departure. The conclusive establishment of these different varieties awaits, then, the further study of their distinguishing characteristics in living, growing material.

Because of the unsettled state of this literature at present a description of the plants discussed below is here offered:

Stellaria aquatica (L.) Scop. Perennial. Roots fine, much branched. Stems ascending, spreading, partly decumbent or nearly erect, especially among other vegetation, 2.3 dm. to 10 dm. in length, more or less four-sided, glabrous below, pubescent and glandular-pubescent above. Leaves decussate, the lower ones petioled, the upper sessile; petioles ciliate, the longest

equal or subequal to the blade, shortening more or less gradually toward the apex of the stem. Lower leaves small, the blades about 1.3 cm. long, sometimes nearly as wide, sometimes longer; upper leaves often 5 cm.–6.3 cm. long, sessile or nearly so, ovate to ovate-lanceolate or oblong-ovate, the base tapering, truncate, rounded or cordate, the apex attenuate, acuminate or acute, the margin often undulate. Leaves (or bracts) of the inflorescence becoming smaller towards the ends of the cyme, as large as the leaves just below at the base of the inflorescence; floral leaves (bracts) and sometimes those just below finely glandular-ciliate and sparingly glandular-pubescent, especially on the veins above and below. Inflorescence typically a dichotomous cyme, some of the branches and flowers sometimes failing to develop; branches of the inflorescence typically terete, glandular-pubescent, the internodes, as in the stem, varying greatly in length. Pedicels glandular-pubescent, reflexed after anthesis and in fruit, the first formed in an inflorescence typically the longest, frequently 3.2 cm. in length, more often less. Sepals glandular-pubescent, ovate to ovate-lanceolate, more or less obtuse, usually about 8 mm. in length in fruit or less, scarious-margined. Petals white, nearly half again as long as the sepals (sometimes more, sometimes less), deeply bifid, lobes oblong, narrow. Stamens usually 10, the 5 sepaline glandular at the base, usually about 2/3 as long as the petals. Styles usually 5, alternate with the sepals; stigmas minutely papillose above, whitish, erect at first, becoming reflexed (with the styles). Capsule ovoid-oblong to ovoid-lanceolate, usually somewhat longer than the sepals, splitting into 5 valves which are often bidentate. Seeds reniform, somewhat flattened, tuberculate.[10]

The essential differences between *S. aquatica* and *S. media* (and other members of the genus also) are very few, while the similarities are striking. In habit the two species are very close; the character and branching of the stems, the shapes of

[10] Material and seed for this study were obtained from wild plants growing along the Bronx River in the New York Botanical Garden. Possibly these plants had "escaped" from a bed in the Garden. Plants for study have also been obtained from the vicinity of Ridgewood, New Jersey. *S. aquatica* is described in our manuals as 'adventive from Europe,' occasional in the eastern states. That it may be of relatively recent introduction might be inferred from the fact that it is not listed in Gray's *Manual*, 6th edition (1889). Taylor in his *Flora of the vicinity of New York* (Mem. N. Y. Bot Gard. **5**: 305. 1915), calls it "a rare and local weed known definitely only near Philadelphia and New York.' House (N. Y. State Mus. Bull. 254: 314. 1924) states that it is 'infrequent, but reported from many localities across the State."

the leaves, the character of the pubescence, especially on the pedicels and calyx, the shape of the sepals and petals, the character of the stigmas, the markings on the seeds—all these are similar in their details in *S. aquatica* and *S. media*, especially the larger varieties of *S. media*. The most obvious differences between *S. aquatica* and the other members of the genus are in the number of the styles and the splitting of the capsules. *S. aquatica* usually has five styles, the other species usually three; but this difference is by no means constant, *S. media* sometimes having four styles, and *S. aquatica* not at all infrequently having that number. The other difference is in the splitting of the capsule, that of *S. aquatica* usually opening into five valves which are frequently two-toothed, while in the other members of the genus the capsule usually splits into six valves. These dissimilarities are sufficient to give *S. aquatica* species rank, but it seems hardly justifiable, in view of the many similarities between this and the other species, especially the larger varieties of *S. media*, to put it in a separate genus.

THE ROOT

A detailed study of the root system and root development is still to be made. However, a preliminary examination of the roots often plants grown in pots shows that the primary root is comparatively well developed near the root collar. Near the surface of the soil large secondary roots are given off, the primary root decreases in size, and in three of the ten plants examined it was difficult to tell, about 1.6 cm. below the surface of the soil, which was the primary and which the secondary roots, since none was of outstanding diameter or growing straight down. In another instance it was easy to trace the course of the primary root as a well developed structure a little over 3 dm. long. The other six plants varied between these extremes. Some of the secondary roots were just as well developed as the primary root. All of these roots gave rise to a great mass of fine thread-like rootlets, and such structures may also develop from the nodes of the stem. These observations have not been very extended and await further and more searching investigation.

Fig. 1. Counterclockwise arrangement of the branches on the stem of *Stellaria aquatica*. Fig. 2. Clockwise arrangement of the branches on the stem of *S. aquatica*. (×1/3)

Fig. 3. Strongly and weakly developed branches each forming a counterclockwise spiral on the same stem of *Stellaria aquatica*. Fig. 4. Reversal of the spiral formed by the branches on the stem of *S. aquatica:* the branch at the second node represented being clockwise to that at the lowest node, the succeeding ones all in counterclockwise spiral; young inflorescence also shown. (× 1/3)

THE STEM AND INFLORESCENCE

With a view to determining the pattern, if any, in the arrangement of the branches, twenty plants raised from seed were watched and the progress of their growth recorded. The leaf arrangement is decussate. All the first formed leaves are petioled; it is only as the plants grow older that sessile leaves appear. The first node, or the first few nodes have as a rule two or more branches. Advancing up the stem of the young plants, however, a point is soon reached at which only one of the two leaves at a node bears a branch in its axil; and these branches originate in spiral fashion, one at each node, so that every fifth node will have a branch approximately above the first. It is obvious that this spiral arrangement can be of two kinds, clockwise as shown in figure 2, and counterclockwise as shown in figure 1. Of the twenty plants studied, eleven showed the clockwise arrangement of the primary branches on the main axis, and nine the counterclockwise.

Tables 1 and 2 show the arrangement of the branches on the lower portions of these twenty plants. The eleven plants in table 1 have the branches arranged in a clockwise spiral on the main stem, the nine in table 2 have the counterclockwise arrangement of the branches on the primary stem. A branch is usually formed in the axil of each of the leaves at the cotyledonary node. These branches have for the sake of convenience been numbered 1 and 2. Plant 12 thus had two branches, one in the axil of each leaf at this first node. The leaves are decussate, and therefore those at the second node are at right angles to those at the first node. The branch at the second node counterclockwise to branch number 1 at the first node has been arbitrarily designated 3; that in similar relation to number 2 has been called 4. This applies to plants in tables 1 and 2. All the other branches on the stem will originate above one of these four (making allowances for twisting of the stem). Thus in plant 12 there were two branches at the third node, one above each of those at the first node; that above number 1 is called 1′, that above number 2 is called 2′. At the fourth node there was a single branch, that above number 3 and therefore designated 3′. Each node is probably potentially capable of producing a branch in the axil of each leaf. Thus at the fourth

node in plant 12 at some later time a branch number 4′ might be produced; therefore the branch at the sixth node is not numbered 4′ but 4″. Not infrequently after a branch has arisen in the axil of a leaf a second branch will develop between the leaf and the first branch. In plant 1 for instance, in addition to branches number 1 and number 2 at the first node there were two others, that between number 1 and its leaf, which is designated 1a, and that between number 2 and its leaf, designated 2a. Each of the branches at a node will again have secondary branches in the axils of some of its leaves; and these secondary branches will also show a clockwise or counterclockwise arrangement on the primary branches. Thus in plant 12 there were two branches at the first node, and on one of these branches the smaller secondary branches were arranged in a counterclockwise spiral, on the other in a clockwise spiral. Therefore branch number 1 in plant 12 has been listed as counterclockwise, branch number 2 as clockwise. If the branch was present but too small to permit the determination of the arrangement of the smaller branches upon it that branch is indicated with a dash; if the arrangement was not clear it is indicated with a question mark; if no branch was present the space is left entirely blank. Some small branches on the main stem at nodes beyond those listed are not given in the tables.

It is evident from the tables that the several lowest nodes usually have a branch (or two branches) in the axil of both of the leaves. In plant 12 the first three nodes each had a branch in the axil of both of the leaves; the three succeeding nodes each had a single branch, and the smaller branches on these three were arranged counterclockwise, counterclockwise, and clockwise, respectively. Here the branches on plant 12 are given for only six nodes; in reality there were more, but they were too small to show the arrangement of the secondary branches upon them and hence are not listed. Of the twenty plants twelve had four branches at the first node, and all twenty had at least one branch in the axil of each leaf. This is of advantage to the plant in spreading over the surface of the soil since the lower branches grow at right angles or more or less opposite to the direction taken by the main stem.

In thirteen plants there was at least one branch in the axil of each leaf of the second node; ten had at least one branch in

TABLE 1

Arrangement of the secondary branches upon the primary branches of the main axis in Stellaria aquatica—the primary branches in each case being arranged in clockwise spiral upon the main axis[a]

PLANT NUMBER	1	2	3	4	5	6	7	8	9	10	11	TOTAL cc	TOTAL c
Arrangement of the primary branches upon the main axis	c	c	c	c	c	c	c	c	c	c	c		
Arrangement of the secondary branches upon the primary branches of the first node	1 cc 1a c 2 cc 2a c	1 cc 1a cc 2 c 2a c	1 c 2 cc	1 c 2 cc?	1 c 1a c? 2 c 2a c	1 c 2 cc	1 c 2 c	1 c 1a cc? 2 c 2a cc	1 cc 1a c? 2 cc 2a cc	1 c 1a — 2 c 2a —	1 cc 2 cc	4 2 6 2	7 3 5 3
Arrangement of the secondary branches upon the primary branches hf the second node	3 c 4 c 4a —	4 cc	3 cc 4 —	3 cc 4 c	3 c 4 c 4a —	3 c 4 c	3 cc 4 c	3 cc	3 c 4 c 4a —	3 cc 4 c	3 cc? 4 cc	6 2	4 7
Arrangement of the secondary branches upon the primary branches of the third node	2′ c 2′a —	1′ cc	1′ c	2′ c	1′ cc?	1′ c 2′ cc	2′ cc	1′ cc 2′ c 2′a —	1′ cc 2′ c 2′a —	1′ cc 2′ c	2′ cc	5 3	2 5
Arrangement of the secondary branches upon the primary branches of the fourth node	4′ c 4′a —	3′ — 4′ c	4′ cc	4′ c	4′ c 4′a —	3′ cc 3′a cc	3′ cc 3′a —	3′ c 3′a —	3′ cc 3′a c	3′ cc	3′ c	4 1 1	2 1 4
Arrangement of the secondary branches upon the primary branches of the fifth node	2″ cc	2″ cc	2″ c	2″ c 2″a —	2″ c 2″a —	1″ cc 1″a —	1″ cc 1″a —	1″ cc	1″ cc 1″a —	1″ c	1″ cc	5 2	1 3

TABLE 1 (continued)

PLANT NUMBER	1	2	3	4	5	6	7	8	9	10	11		
Arrangement of the secondary branches upon the primary branches of the sixth node	3'' c	3'' cc	3'' c 3''a —	3'' cc 4'' cc	3'' c 3''a —	4'' cc 4''a —	4'' cc	4'' cc	4'' cc		4'' cc	2 6	3
Arrangement of the secondary branches upon the primary branches of the seventh node	1''' c	1''' cc	1''' cc 1'''a —	1''' cc	1''' c 1'''a —	2''' c	2''' c	2''' c 2'''a —	2''' cc 2'''a —		2''' c	3 1	2 4
Arrangement of the secondary branches upon the primary branches of the eighth node		4''' cc	4''' c	4''' cc	4''' —	3''' c	3''' cc	3''' cc 3'''a —	3''' c 3'''a —		3''' c	2 2	3 1
Arrangement of the secondary branches upon the primary branches of the ninth node		2'''' cc		2'''' cc			1'''' c	1'''' c	1'''' cc 1''''a —			1 2	2
Arrangement of the secondary branches upon the primary branches of the tenth node				3'''' c			4'''' cc	4'''' cc	4'''' cc			3	1
Arrangement of the secondary branches upon the primary branches of the eleventh node									2''''' c 2''' 'a —				1
												65	64

[a] In the columns of this table c = clockwise; cc = counterclockwise; a ? indicates a doubtful case; and a dash indicates that the branches were too undeveloped to permit determination of the direction of the spiral.

TABLE 2

Arrangement of the secondary branches upon the primary branches of the main axis in Stellaria aquatica—the primary branches in each case being arranged in counterclockwise spiral upon the main axis[a]

PLANT NUMBER	12	13	14	15	16	17	18	19	20	TOTAL cc	TOTAL c	TOTAL TABLES 1 AND 2 cc	TOTAL TABLES 1 AND 2 c
Arrangement of the primary branches upon the main axis	cc	cc	cc	cc	cc	cc	cc	cc	cc			9	11
Arrangement of the secondary branches upon the primary branches of the first node	1 cc 2 c	1 c 1a cc 2 c 2a c	1 cc 1a cc 2 cc 2a —	1 cc 1a c 2 cc 2a cc	1 — 2 c	1 c 1a — 2 cc 2a —	1 cc 2 cc 2a —	1 c 1a c 2 cc 2a c	1 cc 1a — 2 cc 2a —	5 2 6 1	3 2 3 2	9 4 12 3	10 5 8 5
Arrangement of the secondary branches upon the primary branches of the second node	3 c 4 —	3 c 4 c	4 cc	3 c?	3 c	3 cc	3 c 4 c	3 cc 3a — 4 cc 4a —		2 2	5 2	8 4	9 9
Arrangement of the secondary branches upon the primary branches of the third node	1′ cc 2′ c	1′ c 2′ cc 2′a —	1′ c	1′ c		1′ — 2′ cc?	1′ cc 2′ cc	1′ cc 2′ cc 2′a —	1′ c 2′ c 2′a —	3 4	4 2	8 7	6 7
Arrangement of the secondary branches upon the primary branches of the fourth node	3′ cc	3′ c 3′a —	3′ — 3′a —	3′ c 3′a —	3′ c 3′a — 4′ cc?	3′ cc 4′ cc	4′ c	4′ cc 4′a —	3′ — 3′a — 4′ cc 4′a —	2 4	3 1	6 1 5	5 1 5
Arrangement of the secondary branches upon the primary branches of the fifth node	2″ cc	2″ c	2″ cc	2″ c 2″a —	2″ cc	1″ cc?	1″ c	1″ cc 1″a —	1″ c 1″a —	2 3	2 2	7 5	3 5

TABLE 2 (continued)

PLANT NUMBER	12	13	14	15	16	17	18	19	20				
Arrangement of the secondary branches upon the primary branches of the sixth node	4'' c ?	4'' cc	4'' cc	4'' c 4''a —		3'' cc	3'' c	3'' cc 3''a —	3'' c 3''a —	2 2	2 2	4 8	5 2
Arrangement of the secondary branches upon the primary branches of the seventh node		1''' cc	1''' —	1''' c		2''' cc	2''' cc	2''' 2'''a —	2''' cc	1 4	1	4 5	3 4
Arrangement of the secondary branches upon the primary branches of the eighth node		3''' cc	3''' c	3''' 3'''a —			4''' cc	4''' 4'''a —	4''' 4'''a —	1 2	1 1	3 4	4 2
Arrangement of the secondary branches upon the primary branches of the ninth node		2'''' c	2'''' cc	2'''' 2''''a —			1'''' c	1'''' 1''''a —	1'''' cc	2 2	1 1	3 4	3 1
Arrangement of the secondary branches upon the primary branches of the tenth node			4'''' c ?								1	3	1 1
Arrangement of the secondary branches upon the primary branches of the eleventh node													1
										52	41	126	116

[a] In the columns of this table c = clockwise; cc = counterclockwise; a ? indicates a doubtful case; and a dash indicates that the branches were too undeveloped to permit determination of the direction of the spiral.

the axil of each leaf of the third node. At the fourth node however, only four plants had a branch on each side of the stem; at the fifth and sixth nodes none were so characterized. This indicates that there are often four branches at the first node and very frequently there is at least one in the axil of each leaf of the second and third nodes. It should be stated that these plants were grown during the unfavorable winter months, the final observations being made on May 21, when the plants were six months old but not particularly well developed. Field observation shows that six consecutive nodes on vigorously growing plants all with sessile leaves (indicating that they were some distance above the cotyledonary node) each had two branches. A somewhat similar condition is illustrated in figure 3. Only limited conclusions may be drawn from plants grown under the more or less artificial greenhouse conditions. Not all the branches develop at the same time or at the same rate, and further examination at a later date would have yielded further data.

A rather typical plant is number 13 in table 2; it has four branches at the first node, one branch in the axil of each leaf of the second node, one branch in the axil of one of the leaves of the third node and two in the axil of the other, and one branch at each of the succeeding nodes. Other plants show considerable variation from this. In plant 17 the second node has only a single branch, while the third and fourth have two each; in plant 20 the second node is devoid of branches, while there are three at the third and four at the fourth nodes.

In some cases the arrangement of the branches at least apparently changes from one direction to the other. Thus in plant 15 the branch at the third node, 1′, is arranged clockwise with reference to branch number 3, but from there on the branches go up the stem in a counterclockwise spiral. Perhaps it should be stated again that "3′c" (in tables 1, 2) does not mean that branch number 3′ is clockwise in its position with reference to the branch below (in this case it is counterclockwise); it means that the smaller secondary branches on branch number 3′ are arranged in a clockwise spiral on that branch. Whether branch number 3′ is clockwise or counterclockwise with reference to the branch at the node below is shown by the numbers assigned to the branches as described above. In plant 15 the apparent reversal

would be eliminated if there were two branches at the second node instead of one. Figure 4 shows a case similar to this. There the branch at the second node represented is clockwise to that at first, but from there on the branches are arranged in a counterclockwise spiral. Plant number 1 shows just the opposite condition; there branch number 4′ is counterclockwise to branch number 2, but from there on the branches form a clockwise spiral. Here again there would be no reversal if there were a branch in the axil of each of the leaves of the third node, instead of the single branch there.

Branch number 2 of plant 11 had a secondary branch in the axil of each leaf of the first node, and each succeeding node had but a single branch; that at the third node was clockwise to that at the second, that at the fourth node clockwise to that at the third, that at the fifth node clockwise to that at the fourth; but the branch at the sixth node was counterclockwise to that at the fifth and those at the seventh, eighth, ninth, and tenth nodes formed a counterclockwise spiral. This would rather appear like a real reversal. As stated above, each node is probably potentially capable of producing at least one branch in the axil of each of the two leaves and when this occurs the branches are no longer arranged in a single spiral; but even if this occurred in a case like the one described above, they would then form two spirals (each with a reversal) in the order of their appearance; this would also be evident, as shown in figure 3, from the difference in size of the two branches at each node.

A record was also kept of the arrangement of the secondary branches on the primary branches (as in the case just described). In these primary branches each leaf of the first node, almost without exception, had a secondary branch in its axil and the succeeding nodes each had but a single branch, forming a clockwise or counterclockwise spiral as indicated in tables 1 and 2. The tertiary branches on the secondary were mostly in just the same fashion. Thus, while the main stem often had two or more branches at the first three nodes, the primary branches, in the earlier stages at least, usually had two secondary branches only at the first node; and the secondary branches, like the primary, usually had two tertiary branches only at the first node, and one at each node thereafter.

Irregularities were also found on the primary branches. Branch number 4 on plant 4 had a single branch in the axil of each leaf of the first node, but only a single branch at each succeeding node. But the branch at the third node was clockwise to that at the second; that at the fourth was clockwise to that at the third, that at the fifth counterclockwise to that at the fourth, that at the sixth counterclockwise to that at the fifth; the branch at the seventh node was clockwise to that at the sixth, and the succeeding ones all in a clockwise spiral. In this case, in which the branch exhibits two reversals in the spiral, if the branch at the fifth node were on the opposite side of the node, that is clockwise to the branch at the fourth node, the secondary branches would have formed a perfect clockwise spiral. Where there was a change in the direction of the spiral the final direction is the one given in the table.

Not infrequently two branches develop at a node, one in the axil of each leaf, while the nodes above and below have just a single one. Branch number 1 of plant 18 had the usual two branches at the first node, one at the second, third, and fourth nodes, two at the fifth, and one from there on; and the branch at the sixth node was correctly placed with reference to the others—that is the whole branch showed a counterclockwise arrangement of the smaller branches, with one extra branch, which does not enter into the spiral, at the fifth node. This additional branch, not merely here but in other cases as well, was less developed than that on the opposite side of the node. In some instances no branch developed at a node; as is to be expected the branch of the node above usually continues the spiral just as though the missing branch of the vacant node were present.

Sometimes there is a branch in the axil of each of the leaves of a node, with the single branch of the node above situated over the branch of the node below the one with the two branches. Or again there may be two branches, one above the other, with a single branchless node between.

A rather unusual case was found in the arrangement of tertiary branches on a secondary branch of plant 8. The first node had the usual two branches, the succeeding nodes just one. The branch at the third node was counterclockwise to that at the second, that at the fourth counterclockwise to that the third,

that at the fifth clockwise to that at the fourth, the branch at the sixth node counterclockwise to that at the fifth, and that at the seventh clockwise to that at the sixth. If the tertiary branches had originated in a counterclockwise spiral all the way up this secondary branch, with the second, third, and fourth nodes just as they are, the branch of the seventh node would have had its present position, though those at the fifth and sixth would have been different. This branch showed three reversals in six nodes. While Thompson (1917) is undoubtedly correct in saying that phyllotaxy presents no 'subtle mystery' it would seem that cases like this do need further study to reveal their true nature. While it may well be true that each node is capable of producing a branch in the axil of each leaf, the question of why one develops more rapidly than the other must then be answered. When there are two branches at several consecutive nodes, the strongly and weakly developed branches often form two distinct spirals. This by no means exhausts the number or kinds of variations exhibited by the stem and its branches. However the aim is here rather to present the type and the common variations from that type. While the variations have been emphasized, they are really comparatively few.

Tables 1 and 2 show first the arrangement of the branches on the main stem. Of twenty plants there were nine that had these branches in a counterclockwise spiral, and eleven in a clockwise spiral. The nine plants of table 2, all having the primary branches in a counterclockwise spiral on the main stem, had a total of 93 primary branches which were developed well enough to disclose the arrangement of the secondary branches upon them; and of these 93 branches, 52 showed the counterclockwise and 41 the clockwise arrangement of the secondary branches upon the primary. Of these secondary branches 67 were developed far enough to show in turn the arrangement of the tertiary branches upon them—26 were in counterclockwise spiral, 41 in clockwise.

Table 1 shows the eleven plants of the twenty having the primary branches of the main axis arranged in a clockwise spiral. Of these primary branches, 129 were large enough to show how the secondary branches were arranged, and 65 had them in the counterclockwise spiral, 64 in the clockwise. On these eleven plants 75 secondary branches were sufficiently

developed to show the arrangement of the tertiary branches, and of these 35 indicated a counterclockwise, 40 a clockwise spiral. Adding all these together—the 20 main stems, the 222 primary branches, and the 142 secondary branches—187 showed the counterclockwise, 197 the clockwise spiral. Whether this difference is of any significance is very doubtful, though there is a positive correlation with the overlapping of the sepals of the first flower in the inflorescence as will be shown below.

Of the nine well developed branches of plant 17, eight showed the counterclockwise spiral of the secondary branches upon the primary, and only one the clockwise; on the other hand plant 5 had ten branches with the clockwise arrangement, and only one with the counterclockwise. Plants 6, 12, 18, and 20 each had an equal number of primary branches showing the clockwise and counterclockwise arrangement of their secondary branches. There seems to be no regularity in the arrangement of branches showing clockwise and counterclockwise spirals in the plant, though the total number of each in twenty plants was nearly the same.

The leaves of the younger plants are all petioled. Sometimes the leaves even at the base of the inflorescence are very short-petioled. This is unusual however; typically several pairs of leaves below the inflorescence are sessile. Sometimes a very considerable number of nodes, six or eight or more, have sessile leaves before the first flowering node is produced.

There is similar variation in the pubescence. For a distance of two internodes below the inflorescence the stems are as as rule glandular-pubescent. But this varies somewhat, sometimes three internodes, sometimes only one showing this distribution. The glandular character of the pubescence seems less pronounced some distance from the inflorescence. The stems are usually pubescent on all sides (where they are pubescent at all); but sometimes the pubescent internode farthest from the first flower has just a line of hairs, suggesting the condition in *Stellaria media*. The leaves (or bracts) of the inflorescence are glandular-pubescent as well as the branches, as are the leaves at the node below the first flower.

The flower of *S. aquatica* has five sepals, two outer, two inner and one partly outside and partly inside; this quincuncial imbrication is associated with the order of appearance of the

sepals in spiral sequence as described in the older literature (Wichura, 1847; Payer, 1857) and is typical for many dicotyledonous families. There are obviously two possible arrangements which are shown in figures 6 and 7; in these figures the sepals are numbered as in the works cited. When the main axis or one of the branches is terminated by a flower, the orientation of the critical sepal (number 3) is correlated with the clockwise or counterclockwise arrangement of the smaller branches upon the main axis or branch in question. When the arrangement of the branches is counterclockwise, the sepals are oriented as in figure 6 (clockwise); when it is clockwise, the sepals are oriented as in figure 7 (counterclockwise). This seems to hold with but very few exceptions. The first flowers on 153 branches were examined, and in 152 the overlapping of the sepals and the arrangement of the branches were as described above. In figures 6 and 7, *A* and *B* represent the bracts at the base of the pedicel of the flower, and *C* and *D* the bracts or leaves of the node below. Progressing up the stem in a counterclockwise spiral, the branch in figure 6 at the node below the one bearing the flower will be in the axil of the leaf *C*; progressing up the stem in a clockwise spiral, the similar branch in figure 7 will also be in the axil of the leaf *C*. Thus the position of the sepals with reference to the bracts, leaves, and branches is fixed. After anthesis the pedicel will bend, and it bends toward leaf *D* and away from leaf *C* in each case. A branch now appears in the axil of bracts *A* and *B*. This branch produces a single internode and then a node with two bracts, each with their midveins parallel to the midveins of bracts *C* and *D*. The branches bearing these bracts are not vertical like the stem, but oblique as in practically any dichotomous cyme. These points are shown in figure 4; the stem of the plant illustrated there was decumbent, becoming erect toward the apex; therefore in the drawing the inflorescence appears to project toward you. The branches in the axils of bracts *A* and *B* in figures 6 and 7 will be found each to produce a flower at the first node; this terminates each of these branches. But the flower of the branch in the axil of bract *A* in figure 6 will have the sepals originating in clockwise sequence as in figure 6; the flower terminating the branch in the axil of bract *B* in figure 6 will have the sepals originating in counterclockwise

Fig. 5a. An actual inflorescence of *S. aquatica* (× 1/3). Explanation in the text.

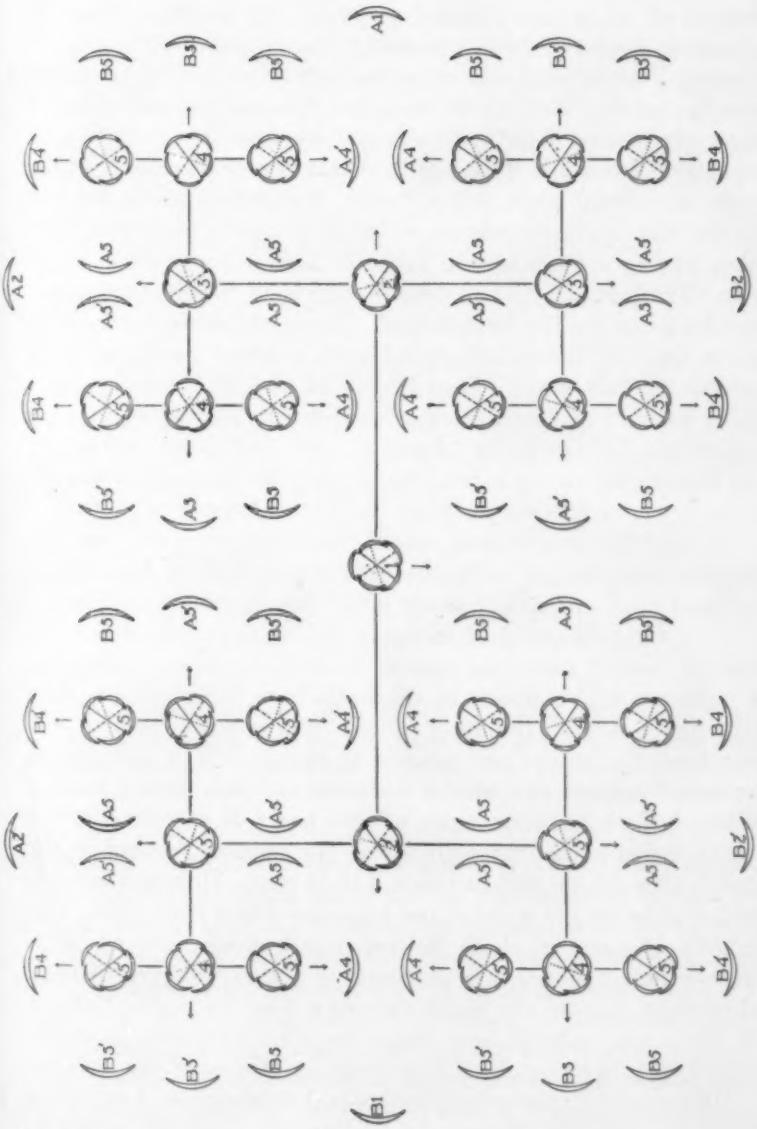


Fig. 5b. Diagram of an inflorescence of *S. aquatica*. Explanation in the text.

Fig. 5a. An actual inflorescence of *S. aquatica* (× 1/3). Explanation in the text.

sequence as in figure 7. The flower terminating the branch in the axil of bract *A* in figure 7 will have the sepals originating in counterclockwise sequence; and that terminating the branch of bract *B* in figure 7 will have the sepals originating in clockwise sequence. Thus these branches are just opposite in this respect in figures 6 and 7. Each of these branches in turn produces two branches at its only node; these also have but a single additional node and a flower, that terminating the one branch having the sepals as in figure 6, that terminating the other having the sepals as in figure 7. This is shown more clearly in the diagram of the cyme in figure 5b, where these relationships can readily be followed. There the flowers are numbered, and the bracts associated with a flower have the same number as that flower. Thus bracts *A*1 and *B*1 are at the base of the pedicel of flower number 1. Flowers having the sepals originating in clockwise sequence are indicated with a ′; and flowers terminating branches arising at the same or similar nodes in the inflorescence have the same number.

A rule for determining these relationships which can be followed is to stand with the reflexed pedicel of the flower (reflexed after anthesis) toward you. The flower of the branch on your right (marked *R* in figure 5a) of the node above the reflexed pedicel will then usually have the sepals overlapping as in figure 7; the flower of the branch on your left (marked *L* in figure 5a) of the node above the reflexed pedicel will then have the sepals overlapping as in figure 6. Furthermore the bract toward you of the node above the reflexed pedicel on the branch on your right will be bract *B* in figure 7; the bract toward you of the node above the reflexed pedicel on the branch on your left will be bract *B* in figure 6. Bracts *A* in both cases will be on the sides of the branches away from you. The pedicels of each of these flowers will become reflexed after anthesis and a branch will originate in the axil of each of their subtending bracts; the same rule can then be applied there. All this is also evident from figure 5b. In that figure the direction of the bending of the pedicels is indicated by arrows.

Exceptions to the general rules laid down above are rather frequent. Of 373 flowers (excluding the first of a cyme) examined while they were open, 24 did not conform. A common condition was to have both of the branches originating

at the same node in an inflorescence terminated by flowers with the same sepaline arrangement, instead of having the sepals of one flower as in figure 6, of the other as in figure 7. In some instances both branches had flowers with the sepals as in figure 6, in others both flowers had the sepals as in figure 7.

The pedicels after anthesis will bend in a definite fashion. If the flower they support has the sepals as in figure 6 they will bend so that they are more or less parallel with the midvein

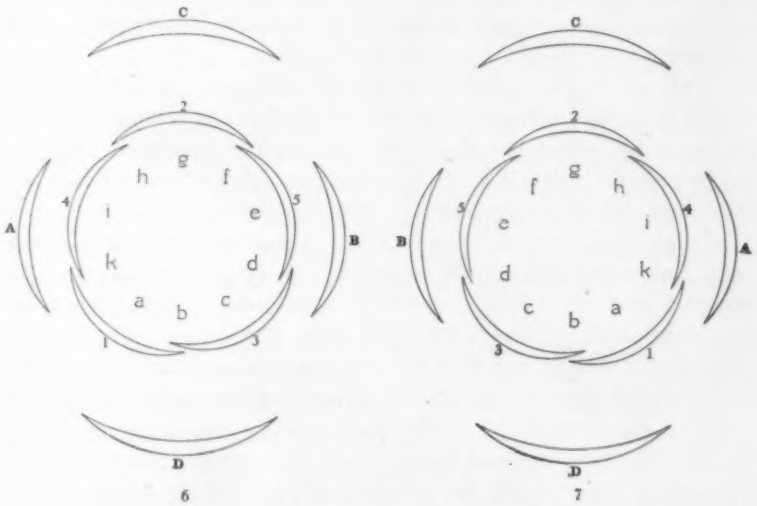


Fig. 6. Arrangement of the bracts and of the sepals in a flower in which the latter originate in clockwise sequence. Fig. 7. Arrangement of the bracts and of the sepals in a flower in which the latter originate in counterclockwise sequence.

of bract *D* of the node below; this is equivalent to saying that if a pedicel supports a flower having the sepals as in figure 6, it will bend so that it is more or less parallel with the midvein of bract *A* of the node below, provided this latter bract subtends a flower with the sepals as in figure 6, since bract *A* in that case becomes bract *D* with reference to that node above. If this flower of the node below has the sepals as in figure 7, then the pedicel supporting a flower having the sepals as in figure 6 will bend after anthesis so that it is more or less parallel with the midvein of bract *B* of that node below.

If, on the other hand, a pedicel supports a flower having the sepals as in figure 7, it will bend after anthesis so that it is more or less parallel with the midvein of bract *D* of the node below; in other words, if a pedicel supports a flower having the sepals as in figure 7, it will bend so as to become more or less parallel with the midvein of bract *A* of the node below, provided this latter bract subtends a flower with the sepals as in figure 7. If this flower of the node below has the sepals as in figure 6, then the pedicel supporting a flower having the sepals as in figure 7 will bend after anthesis so that it is more or less parallel with the midvein of bract *B* of the node below.

This spatial configuration persists throughout the inflorescence; it is shown diagrammatically in figure 5b; it is shown also in figure 5a, which is a drawing of an actual specimen, slightly schematized in that the slight twistings of the internodes have been somewhat disregarded to give greater clarity.

In the inflorescence, as in the vegetative branching, there may be poorly developed branches, or branches may fail to develop entirely. If one of the two branches originating at a flowering node is less developed than the other, it will as a rule be the one terminated by the flower whose calyx is homodromic with that of the flower subtended by the bracts in the axils of which both branches originate. Thus in figure 6 the flower will bend toward bract *D* after anthesis; the branch in the axil of bract *A* will be terminated by a flower whose sepals are homodromic with those of figure 6; that in the axil of bract *B* will be terminated by a flower whose sepals are antidromic with those of figure 6. If one of these two branches is poorly developed it will as a rule be that in the axil of bract *A*. If one of these two branches fails to develop entirely it will also be the one in the axil of bract *A*. If one of the bracts subtending the flower in figure 7 had a weakened branch in its axil it would be bract *A*; and if only one branch develops it will be the one in the axil of bract *B*. This applies to any part of the inflorescence, as may be deduced from figure 5a. There it is evident that if a branch of the inflorescence is poorly developed or fails to develop entirely it will as a rule be the one terminated by a flower whose calyx is homodromic with that of the flower in the axil of whose bract this branch originated. In figure 5a the relative length of the internodes is just as it was in the

actual specimen. Of 51 recorded observations on the failure of one of the branches at a node to develop, only one was not according to the rule formulated above. It is not unusual to find two branches at a node and no flower, a flower and no branches, a flower and one branch, or a flower and one small and one large branch.

THE FLOWER

In comparison with the flowers of *Stellaria media* those of *S. aquatica* are relatively stable with reference to the number of parts. But even in *S. aquatica* there is considerable variation; and since the variability seems to be due in part at least to reduction of parts, a study of a form in which reduction is manifested to only a limited extent might show the early stages of reduction. The data given below have been accumulated with the intention of determining whether the variations occurring in this species are as unordered as might at first appear, and of determining as far as possible the range and limitations of these variations.

No microscopical examination of the stages in the development of the flower has been made in this study to determine the exact relationship between the bracts subtending the flower in the bud, and the sepals. This relation was studied in 65 cases in which the flower had opened; this is not very satisfactory, since there is often a twisting of the pedicel of the flower which obscures the true relationship. The results obtained are in essential agreement with those of Wichura (1846, 1847). Wichura's figures are similar to those of later authors (Eichler, 1878; Warming, 1904; Béguinot, 1920). Eichler's figure has been widely adopted, among others by Pax (1889) and Rendle (1925).

As mentioned above, the overlapping of the sepals may be of two types, depending upon their origin, in clockwise sequence as in figure 6, and in counterclockwise sequence as in figure 7. Branches having the smaller branches upon them in clockwise spiral are terminated by flowers whose sepals originate in counterclockwise sequence; those having the smaller branches in counterclockwise spiral are terminated by flowers whose sepals originate in clockwise sequence. Of 1180 flowers examined, 579 had the sepals originating in clockwise sequence

(as in figure 6), 601 in counterclockwise sequence (as in figure 7). This difference is not very striking, but, as shown above, there were also more branches having the clockwise arrangement of their smaller branches and hence the counterclockwise sequence of the sepals in their first flowers.

The typical flower of *S. aquatica* is pentacyclic, pentamerous, and syncarpous. As indicated in table 3, however, there is considerable variation from this type. The data shown there were obtained from plants growing wild. In the vicinity of the city of New York the flowering period begins about the first week in July and extends to the end of November or beginning of December.

a. *The calyx.* The sepals varied in number from four to six—a rather small range. There is no time during the flowering period in which the number varies greatly. In table 3 there is shown a slight increase in the number of sepals in the beginning of October, but whether this is of any significance is questionable. Of all the parts of the flower the sepals showed the least variation in number—27 flowers with four sepals, 3756 with five, and 7 with six, making a total of 34 with other than five sepals against 3756 with five, or less than one per cent.

The size of the sepals varies greatly, the first formed in an inflorescence usually being about 8 mm. long in fruit. Those later formed are smaller; in flowers with sterile stamens they are often much smaller, and in completely sterile flowers they are sometimes hardly more than a millimeter in length or even less.

Four-sepaled flowers are in general of two kinds: those in which all or nearly all the parts are in multiples of four, and those in which the remaining parts are in multiples of five. In the latter there is obviously a fusion of two sepals, or the formation of one sepal of approximately twice the dimensions of a typical sepal. A study of the vascular system has been made (to be published shortly), which shows that the internal structure is correlated with the two kinds of four-sepaled flowers indicated above, and that the difference is not merely superficial. Figure 16 is a diagram of a flower with four sepals all of the characteristic form; in figure 17, on the other hand, all parts of the flower are regular except one sepal which is obviously double the normal size, and has three stamens and

TABLE 3

Variation in number of floral parts in Stellaria aquatica

DATE	NUMBER OF FLOWERS WITH INDICATED PARTS ON RESPECTIVE DAYS																	Number of flowers examined on respective days
	NUMBER OF SEPALS			NUMBER OF PETALS				NUMBER OF STAMENS					NUMBER OF STIGMAS					
	4	5	6	4	5	6	7	8	9	10	11	12	3	4	5	6	7	
July 8	—	18	—	—	17	1	—	—	1	16	1	—	—	2	8	7	1	18
" 14	—	90	—	—	86	3	1	—	2	84	4	—	—	—	86	3	1	90
" 18	1	99	—	1	98	1	—	—	2	98	—	—	—	4	95	1	—	100
" 20	—	100	—	—	99	1	—	—	—	99	1	—	1	1	97	1	—	100
" 22	1	99	—	1	99	—	—	—	2	98	—	—	—	3	97	—	—	100
" 26	—	100	—	—	99	1	—	—	—	98	2	—	—	4	93	3	—	100
" 28	2	98	—	—	100	—	—	1	2	96	1	—	—	—	94	6	—	100
Aug. 4	1	99	—	1	98	1	—	1	1	95	3	—	—	7	92	1	—	100
" 8	—	99	1	—	94	6	—	—	2	91	6	1	—	2	96	2	—	100
" 17	—	100	—	—	98	1	1	—	1	96	2	1	1	16	82	1	—	100
" 20	—	100	—	—	96	4	—	—	2	92	5	1	—	9	88	3	—	100
" 22	1	100	—	2	99	—	—	—	3	98	—	—	—	3	98	—	—	101
" 25	1	99	—	1	96	3	—	—	2	94	4	—	—	10	86	4	—	100
" 31	—	69	1	—	63	7	—	—	2	63	5	—	1	5	59	5	—	70
Sept. 8	—	37	—	—	37	—	—	—	1	36	—	—	—	1	34	2	—	37
" 9	—	15	—	—	15	—	—	—	—	15	—	—	—	—	13	2	—	15
" 27	—	91	—	—	91	—	—	—	—	90	1	—	1	9	80	1	—	91
" 28	—	88	—	—	87	1	—	—	2	86	—	—	—	9	77	2	—	88
" 29	1	99	—	—	99	1	—	—	1	98	1	—	1	16	83	—	—	100
" 30	1	104	—	1	101	3	—	—	5	100	—	—	3	20	80	2	—	105
Oct. 1	2	81	—	1	82	—	—	—	4	79	—	—	—	6	76	1	—	83
" 2	2	64	—	2	64	—	—	2	1	62	1	—	—	8	56	2	—	66
" 3	1	83	1	—	82	2	1	—	6	78	1	—	1	24	60	—	—	85
" 4	3	110	—	2	110	1	—	1	4	107	1	—	2	7	103	1	—	113
" 5	—	103	1	—	104	—	—	—	2	101	1	—	—	3	100	1	—	104
" 6	1	111	—	1	108	3	—	—	1	110	1	—	—	3	105	4	—	112
" 7	—	50	—	—	50	—	—	—	—	50	—	—	—	1	48	1	—	50
" 8	1	36	—	1	36	—	—	—	2	35	—	—	—	4	33	—	—	37
" 9	1	107	1	—	109	—	—	1	1	107	—	—	1	4	104	—	—	109
" 12	—	119	—	—	119	—	—	—	—	119	—	—	—	1	110	8	—	119
" 13	—	132	1	—	132	1	—	—	2	129	2	—	—	4	124	5	—	133
" 14	1	106	—	—	106	1	—	—	—	106	1	—	—	7	94	6	—	107
" 16	—	98	—	—	98	—	—	—	1	97	—	—	—	6	90	1	1	98
" 18	—	44	—	—	43	1	—	—	—	44	—	—	—	—	42	2	—	44
" 20	1	90	—	1	90	—	—	—	1	90	—	—	—	3	86	2	—	91
" 23	1	98	1	1	98	1	—	—	—	100	—	—	—	3	92	4	1	100
" 27	—	53	—	—	53	—	—	—	—	53	—	—	—	9	44	—	—	53
" 28	—	94	—	—	93	1	—	—	—	94	—	—	—	6	86	2	—	94
" 31	—	43	—	—	43	—	—	—	1	42	—	—	—	8	34	1	—	43
Nov. 2	—	64	—	—	64	—	—	—	—	64	—	—	—	7	54	3	—	64
" 4	—	77	—	1	76	—	—	—	—	77	—	—	—	8	65	4	—	77
" 7	2	60	—	1	60	1	—	—	2	56	4	—	—	7	48	7	—	62
" 10	—	49	—	—	49	—	—	—	—	48	1	—	1	3	43	1	1	49
" 11	—	46	—	—	46	—	—	—	1	44	1	—	—	2	42	2	—	46
" 14	—	42	—	—	42	—	—	—	—	41	1	—	—	1	41	—	—	42
" 17	—	10	—	—	10	—	—	—	—	10	—	—	—	—	9	1	—	10
" 18	—	20	—	—	20	—	—	—	—	20	—	—	—	—	19	1	—	20
" 19	—	15	—	—	15	—	—	—	—	15	—	—	—	—	15	—	—	15
" 21	—	15	—	—	15	—	—	—	—	15	—	—	—	—	15	—	—	15
" 22	—	10	—	—	10	—	—	—	1	9	—	—	—	—	10	—	—	10
" 25	—	7	—	—	7	—	—	—	—	7	—	—	—	—	7	—	—	7
" 27	1	5	—	1	5	—	—	1	—	5	—	—	—	—	6	—	—	6
" 28	1	4	—	1	4	—	—	—	1	4	—	—	—	—	5	—	—	5
Dec. 1	—	6	—	—	6	—	—	—	—	6	—	—	—	—	5	1	—	6
Totals	27	3756	7	20	3721	46	3	7	62	3667	51	3	13	256	3409	107	5	3790

a petal opposite it instead of a single stamen. These diagrams, as well as all the others, are representations of actual flowers, and the two just discussed are not uncommon. Figure 18 shows a case in which all four sepals are apparently normal, none is appreciably larger than the others; whether one of the sepals was supplied with double the amount of vascular tissue, whether one of them has become entirely petaloid, or whether the internal parts correspond with the external appearances remains to be investigated. It is not unusual in four-sepaled flowers to have only nine stamens, and sometimes three-lobed petals occur.

Two additional factors support the view that the large sepals described above are in reality two sepals fused; first the occurrence, rather rarely, of a single large sepal more or less two-lobed, indicating partial fusion; and secondly the fact that different sepals are apparently fused at different times. The commonest arrangement in flowers having four sepals, one larger than the others, is to have two inner sepals alternating with two outer, sepal 3 of figures 6 and 7 being apparently eliminated. One of the inner sepals then is twice its normal size, suggesting that there has been a fusion of sepals 3 and 5 of both figures. This is illustrated in figure 17. In two flowers the calyx consisted of an outer sepal, then (going in clockwise direction) an oblique one, like sepal 3, this being double, then an inner sepal, then another oblique one, suggesting that sepals 4 and 2 in figure 6 had fused. In another flower the arrangement, in clockwise fashion, was an oblique sepal (double), an outer sepal, another oblique sepal, and an inner sepal, indicating that sepals 2 and 4 of figure 7 had fused; all the other parts of the flower were in multiples of five. This evidence indicates strongly that there can be fusion of different sepals, the oblique one (number 3) with an inner, or an outer with an inner sepal.

Sometimes in the calyx of *S. aquatica* there are sepals that are partially petaloid. This may be evident as merely a fine white line appearing in the center or on one side of the sepal; in other cases there are two white lines; from this there are all gradations to that condition in which the sepal is a two-lobed structure, one lobe of which is white, to that in which practically the whole sepal is white and two-lobed with just a trace of

green. The sepal affected in 40 flowers in which one was more or less petaloid in character, was in each case one of the inner ones; and of the 40 instances, sepal number 4 was affected 12 times, sepal number 5, 28 times; this shows that the sepal nearest the petaline whorl in origin most frequently becomes more or less petaloid. One flower (fig. 18) was observed having four sepals all apparently normal, but between two there were three petals; it is possible that the middle petal of these three was a transformed sepal; the positions of the styles would substantiate this though there were only nine stamens. This is merely a suggestion and awaits further histologic investigation. This discussion of the petaloidy of the sepals is not offered as anything new; nevertheless it is intimately associated with the question of the origin of the perianth, a problem that has been debated up to the present but not wholly settled.

b. *The corolla*. Greater variation in both range and numbers was shown by the petals than by the sepals. There were 20 flowers with four petals, 3721 with five, 46 with six and 3 with seven. Here again there seems to be no time during the flowering period at which the number of petals is decidedly greater or less than at any other, though there was considerably more variation in August than at any other time; but the number of individuals was not very large for such a study.

By means of sepal 3 it is possible to determine the position in the flower in which additional petals most frequently occur. The number of times that additional petals occurred in each position in figures 6 and 7 is shown in tables 4 and 5. It is evident that additional petals very rarely occur opposite the sepals. Supernumerary petals usually occur between sepals 2 and 4, at position *h* in both figures. The additional petals at *h* numbered 32, those at all the other positions combined totaled only 18. The occurrence of additional petals in position *h* is shown in figures 19, 20, 21, and 23. It is thus possible to predict where in the flower extra petals will usually occur.

Of 46 flowers with one additional petal, 27 also had an additional stamen opposite that petal, fourteen had just one stamen associated with the two petals, four had no stamens with either petal, and one had three stamens with the two petals. In the greater number of cases, then, there is an additional stamen opposite an additional petal. This rather emphasizes

the close relationship between stamens and petals. Limited data indicate that when a petal is missing the stamen usually develops just the same. But this point needs further investigation.

Three flowers having seven petals showed considerable variation in the distribution of the latter; one flower had two additional petals between the same two sepals, another had two on each side of a single sepal (instead of just one), and the third had six sepals with two petals between one pair.

TABLE 4

Number of additional petals and additional, missing, and sterile stamens in each position in flowers having the sepals arranged in counterclockwise sequence as in figure 7

SEPAL NO.	1		3		5		2		4		TOTAL NUMBER	
POSITION IN FLOWER	a	b	c	d	e	f	g	h	i	k	Alternate with sepals	Opposite sepals
Additional petals		4		4			2	22	1	1	31	3
Additional stamens	1	4		2	3		1	19	10	1	26	15
Missing stamens	1	2		2	2	13	1	3		1	21	4
Sterile stamens	103 (108.5)	109 (114.8)	64 (67.4)	63 (66.4)	52 (54.8)	101 (106.4)	92 (96.9)	119 (125.4)	90 (94.9)	141 (148.5)	533	401

Petals having three lobes instead of two not infrequently occur. Sometimes one of the three lobes is smaller than the others (usually the central one); in other cases the three are all of approximately equal size. Of five five-sepaled flowers like that in figure 7, having a three-lobed petal, four had it in position *h*. Of four flowers like that in figure 6, three had the three-lobed petal at *h*, making a total of seven out of nine possible cases at *h*; the other two positions were *d* in figure 7 and *b* in figure 6. The position *h* is the one in which additional petals also most frequently occur. There were also two four-sepaled flowers having three-lobed petals. Of eleven flowers having three-lobed petals, six had a single stamen associated with the three-lobed petal, five had two stamens, showing that it is not unusual to have an increase in the number of stamens associated with an increase in the petal quantity.

Simple petals (not two-lobed) are also found in *S. aquatica*.

There were nine such cases observed, one occurring at points *h* and *b* in figure 7, one at *h* and *k* and five at *d* in figure 6. Such petals were associated with a single stamen, as in the case of normal petals.

In addition to these non-lobed petals, others sometimes occur in which the lobes are of unequal size. Then too there are flowers in which the petals are much reduced in size. This is particularly true of the flowers with sterile stamens produced especially toward the end of the year; in these the corolla may be no larger than the calyx, and sometimes it is decidedly smaller.

TABLE 5

Number of additional petals and additional, missing, and sterile stamens in each position in flowers having the sepals arranged in clockwise sequence as in figure 6

SEPAL NO.	1		4		2		5		3		TOTAL NUMBER		TOTAL tables 4 and 5	
POSITION IN FLOWER	a	k	i	h	g	f	e	d	c	b	Alternate with sepals	Opposite sepals	Alternate with sepals	Opposite sepals
Additional petals		3		10				3			16	0	47	3
Additional stamens			6	9			1	1	1		10	8	36	23
Missing stamens		2		2	2	5	1			2	11	3	32	7
Sterile stamens	115	135	99	118	109	112	65	68	69	94	527	457	1060	858

Sometimes one or several of the petals are reduced, while the others are of the normal size. There may thus be petals of different sizes in the same flower. The most extreme reduction takes place in the minute totally sterile flowers in which the petals are sometimes reduced practically to the vanishing point.

Petals more or less green (usually less) have been observed. This is a suggestion of sepaline character. Further suggestion of the relationship between sepals and petals is offered by the occurrence of two-lobed sepals with one lobe green and the other white, with the petal missing which should be adjacent to the white half of the sepal. Whether such instances are cases of fusion between members of the two whorls remains to be established for *S. aquatica*.

Anthers sometimes occur on petaloid structures. This was observed in only four cases in this species, and in each of these the petaloid structure was in addition to the usual number of petals. In one instance the stamen, anther and filament, were apparently fused with a petaloid structure, as all were distinguishable. In the other three the anthers were simply borne on a petaloid outgrowth, simple in two cases, two-lobed like a petal in the other. In each instance there was the usual complement of ten stamens also, so that these structures were supernumerary with regard to both petals and stamens. Whatever interpretation may be placed upon them, their occurrence further emphasizes the close relationship between stamens and petals.

c. *The androecium*. The number of stamens varies decidedly more than that of the sepals and petals, as indicated in table 3. Of 3790 flowers 7 had eight stamens, 62 had nine, 3667 had ten, 51 had eleven and 3 had twelve. The ten usual stamens are arranged five opposite the sepals and five opposite the petals. In the floral diagrams below they have been drawn as two whorls in the obdiplostemonous arrangement. The question of obdiplostemony is to be considered further in the study of the internal structure of the flower. Each of the antesepalous stamens is provided with a gland at the base of the filament.

As indicated in tables 4 and 5 the positions in each of the two kinds of flowers in which additional stamens most usually occur are *h* and *i*. Of 41 supernumerary stamens occurring in flowers having the sepals in counterclockwise sequence 19 were at *h* and 10 at *i*; and of 18 additional stamens in flowers in which the sepals originated in clockwise sequence 9 were at *h* and 6 at *i*. Out of a possible 59, 44 of the additional stamens occurred in these two positions; additional stamens at *h* were more frequent than at *i*. The close proximity of these two positions may also be of significance. Figures 19, 20, 24, 25, and 26 illustrate the occurrence of extra stamens in these positions.

Position *h* is important, then, because it is there that additional petals, three-lobed petals, and additional stamens most frequently occur. Furthermore position *h* with the center of sepal 3 establishes an axis passing through the center

of the flower. This axis corresponds in position with axes of symmetry in the flowers of *Hyoscyamus albus*, *Stigmaphyllon*, *Hiptage Madablota*, *Camarea triphylla*, *Trigonia simplex*, *Hirtella triandra*, *Couepia macrophylla*, *Licania macrophylla*, *Parinarium Gardneri*, and *Hirtella Sprucei* (Eichler 1875, 1878).

Of 36 supernumerary stamens opposite petals, 27 were associated with an additional petal, 4 with a three-lobed petal (the fifth three-lobed petal mentioned above being in a flower having nine stamens) and in only 5 cases were two stamens associated with a single petal. This again emphasizes the close relationship between these structures. It is not unusual to find two stamens opposite a sepal and then there is no additional petal or sepal.

The position at which a stamen may most easily be lost also seems to be relatively fixed. As indicated in tables 4 and 5 position *f* more frequently is without a stamen than any other. In 18 cases out of 39 this was the position affected. In only 7 instances out of 39 was a sepaline stamen lost. The failure of a stamen to develop in position *f* is shown in figures 27 and 28. With the center of the flower position *f* establishes another axis; this is similar in position with axes of symmetry in the flowers of *Petunia nyctaginiflora*, *Schizanthus retusus*, *Salpiglossis sinuata*, *Anacardium occidentale*, *Saxifraga granulata*, *Saxifraga sarmentosa*, and *Cassia caroliniana* (Eichler 1875, 1878). Through these axes, shown in figure 5b, which are established in the flower with a certain amount of constancy, the flower seems to be losing its regularity and taking on a form which, to a certain extent at least, is zygomorphic with respect to certain whorls.

Eight stamens have been found in four- and five-sepaled flowers, nine in four-, five-, and six-sepaled flowers, ten in four- and five-sepaled flowers, eleven and twelve in five- and six-sepaled flowers.

When a stamen is missing it frequently happens that the filament of one of the adjacent stamens, instead of being more or less in a plane with the axis of the flower, leans over into the space in which the stamen is missing, the anther sometimes being extended beyond the place that the missing stamen would occupy.

Sterility in the androecium. Flowers of *S. aquatica* frequently

have one or more of the stamens modified into staminodia. There are all grades in the sterility of the stamens. All the normal anthers examined showed some small pollen grains. From this condition of normal minimum which seems to prevail in all flowers there are examples of all grades in the increase in the proportion of sterile grains to cases in which the majority of the grains in an apparently normal anther are small and shrivelled. Likewise there are stamens which have normal anthers with the usual proportion of normal grains but with the filament shortened; or the filament may be of the usual length but the whole anther shrivelled and dry in appearance. Such anthers have a fraction at least and more usually all of the grains shrivelled. There are examples of all stages in the decrease in the size of the anthers, from those only slightly below normal to those in which the anther consists merely of an extremely minute membranous structure without pollen grains; sometimes there appears to be a yellow mass within the anther, not developed into grains; sometimes this too is lacking. This reduction of the anthers is accompanied as a rule by a reduction in the size of the filaments, so that sterile stamens are often very small structures barely visible to the naked eye; sometimes they appear merely as minute microscopic papillae. It occasionally happens that half an anther is normal with normal grains, the other half small with shrivelled grains.

Preliminary germination tests which have been made indicate that the small shrivelled grains do not germinate under conditions identical with those permitting the formation of tubes in the normal grains.

Tables 4 and 5 show the positions of the staminodia in flowers having from one to nine stamens sterile; all are here grouped together except those having all ten stamens sterile. Table 4 was compiled from 305 flowers having a total of 934 staminodia, or 3.06 staminodia per flower; table 5 gives data from 300 flowers having a total of 984 staminodia or 3.28 staminodia per flower, giving an average of 3.17 staminodia per flower.

In the flowers examined the production of reduced stamens was more common in the antepetaline than in the antesepaline whorl—a total of 1060 sterile stamens in the former to 858

TABLE 6

Sterile stamens in Stellaria aquatica

DATE	NUMBER OF FLOWERS WITH THE FOLLOWING NUMBER OF STERILE STAMENS										Number of flowers with sterile stamens	Number of sterile stamens on respective days	Number of flowers examined on respective days	Per cent of flowers examined with sterile stamens	Total number of stamens on respective days	Per cent of stamens sterile
	1	2	3	4	5	6	7	8	9	10						
July 8	—	—	—	—	—	—	—	—	—	—	0	0	18	0	180	0.0
" 14	1	—	—	—	—	—	—	—	—	—	1	1	90	1	902	0.1
" 18	—	—	—	—	—	—	—	—	—	—	0	0	100	0	998	0.0
" 20	6	—	—	—	—	—	—	—	—	—	6	6	100	6	1001	0.6
" 22	1	1	1	3	—	2	—	—	—	2	10	50	100	10	998	5.0
" 26	—	—	1	2	1	—	—	—	—	—	4	16	100	4	1002	1.6
" 28	3	3	3	—	—	2	—	—	—	—	11	30	100	11	997	3.0
Aug. 4	4	—	—	1	1	—	2	—	—	—	8	27	100	8	1000	2.7
" 8	2	—	—	1	1	2	—	1	—	1	8	41	100	8	1006	4.1
" 17	7	4	1	3	1	1	—	1	—	4	22	89	100	22	1003	8.9
" 20	—	1	1	1	—	1	—	—	—	1	5	25	100	5	1005	2.5
" 22	8	6	3	4	3	3	1	—	1	3	32	124	101	32	1007	12.3
" 25	5	1	1	—	2	—	—	—	—	—	9	20	100	9	1003	2.0
" 31	—	1	1	—	—	—	—	—	—	—	2	5	70	3	703	0.7
Sept. 8	1	5	4	1	1	2	1	3	1	1	20	94	37	54	369	25.5
" 9	3	2	—	—	1	1	—	—	—	3	10	48	15	67	150	32.0
" 27	4	6	1	2	—	1	—	—	2	1	17	61	91	19	911	6.7
" 28	3	4	1	3	2	—	2	—	3	2	20	97	88	23	878	11.0
" 29	8	3	2	2	1	—	1	1	—	—	18	48	100	18	1000	4.8
" 30	5	—	3	3	—	—	—	—	—	—	11	26	105	10	1045	2.5
Oct. 1	5	—	6	4	3	1	2	—	—	—	21	74	83	25	826	9.0
" 2	2	4	4	—	—	1	—	3	—	—	14	52	66	21	656	7.9
" 3	7	—	3	2	3	1	—	—	—	1	17	55	85	20	845	6.5
" 4	11	3	2	1	—	1	3	—	—	—	21	54	113	19	1125	4.8
" 5	7	5	2	4	1	—	—	1	—	1	21	62	104	20	1039	6.0
" 6	6	4	1	1	1	1	—	—	—	—	14	32	112	13	1120	2.9
" 7	7	1	2	—	1	—	1	—	—	—	12	27	50	24	500	5.4
" 8	2	1	—	—	—	—	1	1	—	1	6	29	37	16	368	7.9
" 9	9	2	4	3	1	2	1	6	1	3	32	148	109	29	1087	13.6
" 12	6	7	3	—	1	1	1	2	—	2	23	83	119	19	1190	7.0
" 13	12	3	2	3	—	—	1	—	—	1	22	53	133	17	1330	4.0
" 14	2	1	1	1	2	1	—	—	—	—	8	27	107	7	1071	2.5
" 16	3	—	—	2	1	—	2	1	—	—	9	38	98	9	979	3.9
" 18	5	6	3	2	2	—	1	—	—	—	19	51	44	43	440	11.6
" 20	7	3	1	1	—	—	—	—	—	—	12	20	91	13	911	2.2
" 23	5	4	1	1	1	1	—	—	—	—	13	31	100	13	1000	3.1
" 27	4	—	1	1	—	—	1	1	—	—	8	26	53	15	530	4.9
" 28	7	3	1	1	1	—	—	—	—	1	14	35	94	15	940	3.7
" 31	3	1	5	1	3	1	—	—	2	3	19	93	43	44	429	21.7
Nov. 2	1	5	4	3	3	3	1	1	—	—	21	83	64	33	640	13.0
" 4	4	6	1	2	1	—	2	2	—	6	24	122	77	31	770	15.8
" 7	2	7	2	2	—	1	2	—	—	2	18	70	62	29	622	11.3
" 10	4	2	1	1	4	1	1	1	1	10	26	165	49	53	491	33.6
" 11	2	6	3	2	3	3	1	1	—	3	24	109	46	52	460	23.7
" 14	7	6	2	3	2	1	2	1	—	—	24	75	42	57	421	17.8
" 17	6	—	—	1	—	—	—	—	—	—	7	10	10	70	100	10.0
" 18	3	3	—	3	1	—	—	1	—	—	11	34	20	55	200	17.0
" 19	3	1	2	—	1	1	—	—	—	2	10	42	15	67	150	28.0
" 21	2	1	1	2	—	1	—	—	1	2	10	50	15	67	150	33.3
" 22	—	—	—	1	—	—	—	1	1	1	4	31	10	40	99	31.3
" 25	1	1	1	—	—	—	1	2	1	—	7	38	7	100	70	54.3
" 27	2	—	—	1	—	—	1	—	—	—	4	13	6	67	58	22.4
" 28	1	1	—	1	—	—	—	—	—	1	4	17	5	80	49	34.7
Dec. 1	1	—	—	—	—	—	1	—	—	2	4	28	6	67	60	46.7
Totals	210	124	82	76	50	37	33	31	14	60	717	2685	3790	19	37884	7.1

in the latter. Tables 4 and 5 show further the number of these in each position in the flower, the letters being the same as in figures 7 and 6. In ascending order with reference to the number of sterile stamens the positions in table 4 are *e*, *d*, *c*, *i*, *g*, *f*, *a*, *b*, *h*, *k*; the order in table 5 is *e*, *d*, *c*, *b*, *i*, *g*, *f*, *a*, *h*, *k*. These orders, excepting *b* are the same. The total number of sterile stamens taken into account in tables 4 and 5 is 1918, of which 934 are in table 4 and 984 in table 5. Therefore each of the

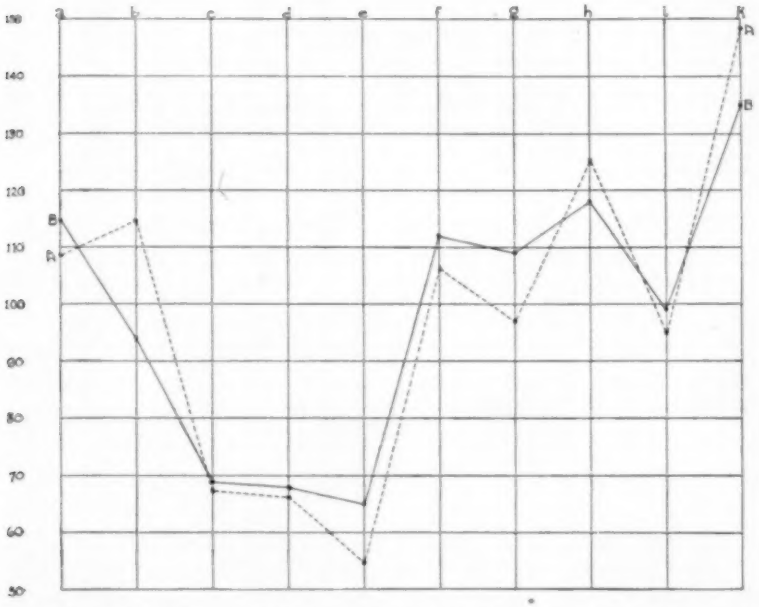


Fig. 8. Frequency of the occurrence of sterile stamens, *AA* of the positions of the flower having the sepals as in figure 7, *BB* of the positions of the flower having the sepals as in figure 6.

figures in table 4 was multiplied by 984/934, and the values obtained are recorded in parentheses. Then these values and those of table 5 were plotted as shown in figure 8. There *AA* is the graph for table 4, *BB* the graph for table 5. The general similarity of these curves is quite evident, the greatest inconsistency being at *b*. Why certain positions should have more or fewer sterile stamens, in definite ratio with the other positions, is not evident.

Table 6 gives the number of flowers with 1–10 sterile stamens for different days during the flowering period. Thus on July 22, there was one flower with one sterile stamen, one with two, one with three, three with four, none with five, two with six, none with seven, eight and nine, and two with all ten stamens sterile, giving a total of ten flowers showing one or more sterile stamens and a total of 50 sterile stamens for those ten flowers. The total number of flowers examined on that day was 100 and the total number of stamens on those 100 flowers was 998. Therefore the percentage of flowers showing one or more sterile stamens was

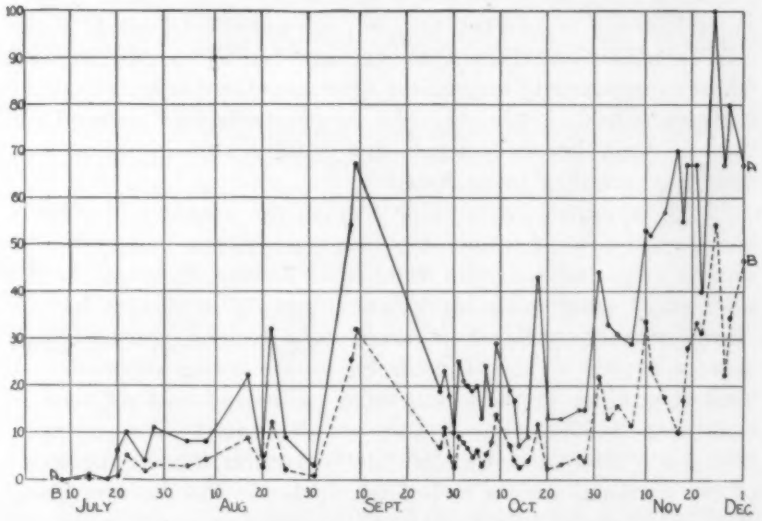


Fig. 9. Advancing seasonal staminal sterility: *AA* the per cent of the total number of flowers examined on the respective days with one or more sterile stamens, *BB* the per cent of the total number of stamens on the respective days sterile.

10; the percentage of the total number of stamens sterile on that day was 5.0. These percentages are shown plotted in figure 9, *AA* being the percent of the total number of flowers examined on the respective days with one or more stamens sterile, *BB* the per cent of the total number of stamens sterile each day. The average of the first taking the total number of flowers into account, was 19 per cent, that of the second 7.1 per cent.

In general there is a gradual increase in the number and

proportion of sterile stamens toward the end of the season. The only striking exception to this general increase was on September 8 and 9. It should be stated that torrential rains during the first week in September washed away all but the older and lower portions of a few plants; this also explains the small number of flowers examined on those days. Some of the other smaller deviations are less easily explained. The plants were growing wild and not all in the same place; the flowers were taken at random. Those for instance listed for October 18 were found in a more exposed place, and were apparently more liable to insect attack than the others. Some variations are to be expected, but the general trend, with the one exception mentioned above, can hardly be questioned. There is apparently a gradient here associated with metabolic activity (Child, 1915a, b). The terms sterile and reduced are used in their broadest sense, any stamen showing some evidences of sterility being listed.

It is apparent from table 6 that the number of flowers having just a single stamen sterile is greater than that of flowers having two, and that the number of flowers decreases as the number of staminodia increases, excepting in flowers having all ten stamens sterile; there, there was a decided increase. Such flowers having all the stamens sterile are really imperfect. A limited number of these was cross pollinated and set seed in each case, while similar flowers not pollinated did not. Both Henslow (1888) and Rendle (1925) ascribe the derangement of the staminal whorls to low temperature, Rendle remarking that in *S. media* 'the number of abortive stamens is greater the colder the time of year.' This is in agreement with the results given above. However they go on to say that in the Alsinoideae the pistillate flowers are in bloom chiefly at the beginning of the flowering period. This does not hold for *S. aquatica*. Plants growing wild in the vicinity of the city of New York have been watched for several years. They did not come into bloom much if any before the first week in July. Of a total of 608 flowers gathered at random during the month of July only two had all ten stamens sterile, while in November of 428 flowers 27 had all the stamens sterile. This indicates that for *S. aquatica* the condition is just the reverse of that given by Henslow and Rendle for the Alsinoideae.

d. *The gynoecium.* The styles and carpels of *S. aquatica* are typically five in number. Bentham (1861, 1862) however, reported the occurrence of three-styled flowers in India and temperate Asia. Béguinot (1914) gives the variations in the number of styles from six to two, four and three being the most common after five. He remarks that the percentage of flowers with four styles is greater in June and July and less in October and November.

The number of styles in flowers recorded in table 3 varied from three to seven, there being 13 flowers with three, 256 with four, 3409 with five, 107 with six and 5 with seven. The proportion of four-styled flowers here is less than that reported

TABLE 7

Variation in number of styles according to months

MONTH	NUMBER OF FLOWERS EXAMINED	NUMBER OF 4-STYLED FLOWERS	PER CENT OF FLOWERS 4-STYLED	NUMBER OF 6-STYLED FLOWERS	PER CENT OF FLOWERS 6-STYLED
July	608	14	2.3	21	3.4
August	671	52	7.7	16	2.4
September	436	55	12.6	9	2.1
October	1641	107	6.5	41	2.5
November	428	28	6.5	19	4.4
Totals	3784	256	6.8	106	2.8

by Béguinot, and the proportion of six-styled flowers much greater. The four-styled flowers examined by Béguinot varied in number from approximately 28 per cent of the total number in June and July to 13.24 per cent in October and November, and only 3 out of 814 flowers were six-styled. In table 7 the data given in table 3 are arranged according to months; in contrast to the figures for the Mediterranean region the data for New York indicate a variation in the proportion of four-styled flowers from 2.3 per cent in July to 12.6 per cent in September, the proportion of the total number of flowers four-styled being 6.8 per cent. Of course the variation in the months, if seasonal, would not correspond with that in Italy and the Mediterranean countries. The percentage of six-styled flowers varied from 2.1 to 4.4 per cent, the proportion of the total

number of flowers six-styled being 2.8 per cent. Thus the percentage of six-styled flowers, while low, was not entirely negligible, and in July actually exceeded that of the four-styled flowers. The proportion of three-styled flowers found is less than that reported by Béguinot.

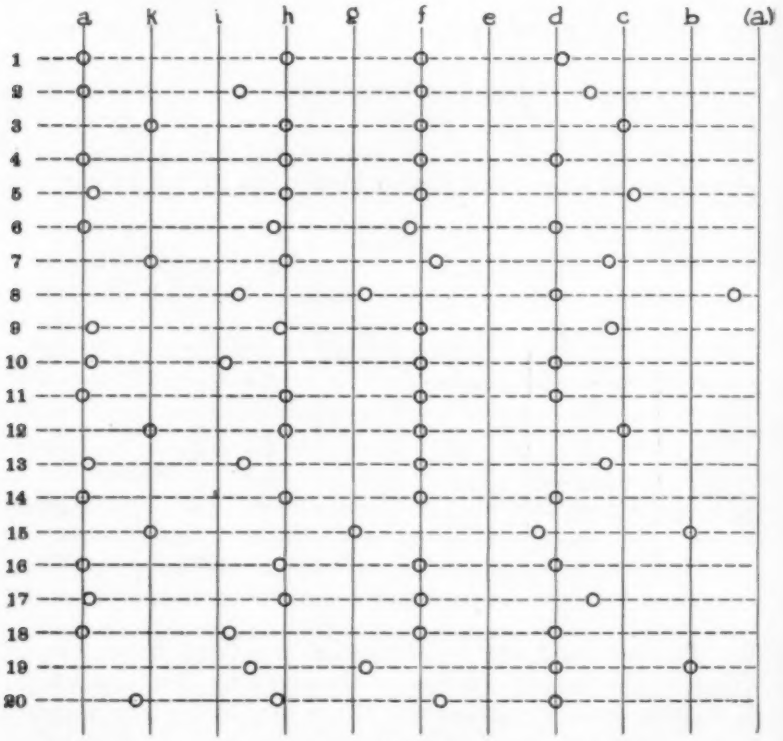


Fig. 10. Position of the styles in 20 four-styled flowers having the sepals overlapping as in figure 6.

The five styles of *S. aquatica* typically alternate with the five sepals i.e. the carpels are opposite the petals. Therefore in four- and six-styled flowers there must of necessity be some asymmetry. In figures 10 and 11 the positions of figures 6 and 7 are plotted and lettered as in those figures. The circles in those figures represent the styles, each of the flowers there diagrammed having four. Figure 10 thus shows the positions of the styles in 20 four-styled flowers; in figure 11, 21 flowers are represented.

In the normal five-styled flower there is a style in positions *b*, *d*, *f*, *h*, *k*. The data here presented are subject to some error because of the bending of the styles and stigmas. However by examining the styles near the base this difficulty is partly overcome at least. This procedure was followed. The splitting of the capsules was in many cases compared with the positions

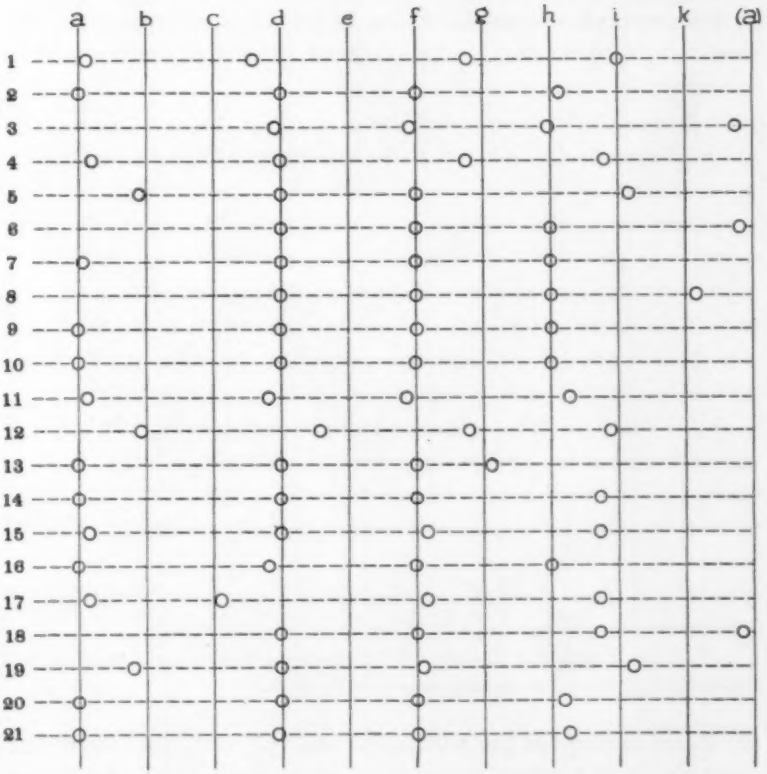


Fig. 11. Position of the styles in 21 four-styled flowers having the sepals overlapping as in figure 7.

of the styles (by means of records) and there was general agreement in the major lines of splitting, with some exceptions. From figures 10 and 11 it is evident that in a general way the styles primarily affected in four-styled flowers are those in positions *b* and *k*; these are usually replaced by a single one

which varies somewhat in its position but tends to be at or near position *a* (shown also in figure 29). This holds for flowers with the sepals overlapping as in figures 6 and 7 in equal measure. Position *a* with the center of the flower also establishes an axis in the flower; this axis is identical in position with the one established by the frequent loss of a stamen in position *f*.

Figures 12 and 13 show the positions of the styles in six- and seven-styled flowers. From figure 13 it appears that the single style at *d* tends to be replaced by one at both *c* and *e*,

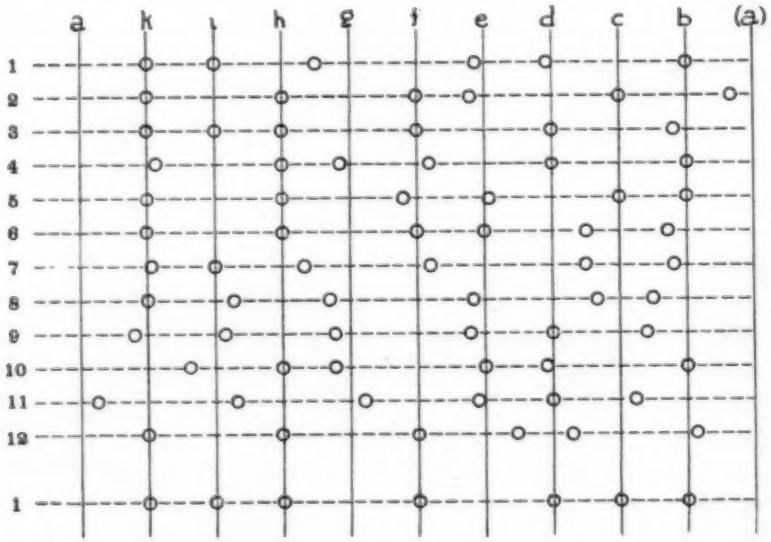


Fig. 12. Position of the styles in 12 six-styled flowers and 1 seven-styled flower having the sepals overlapping as in figure 6.

thus accounting for the additional one (fig. 30). Of course the position of the other styles here as in four-styled flowers is also somewhat affected, but that seems to be the general rule. This is not so evident from figure 12. These observations on the styles, especially in the six- and seven-styled flowers, are of a preliminary nature. There seems then to be another axis of symmetry established in six-styled flowers, passing through *d*. This is similar in position to axes of symmetry in the flowers of *Impatiens glanduligera*, *Impatiens tricornis*, *Aesculus Hippocastanum*, *Urvillea*, *Serjania*, *Salvertia convallariodora*,

Vochysia oppugnata, *Qualea macropetala* and *Myoporum parvifolium* (Eichler, 1875, 1878). None of these axes established in the flower of *S. aquatica* with reference to missing and additional parts correspond with the axis of symmetry most usually occurring in flowers with a five-parted calyx, namely that passing through *b* and the center of the flower.

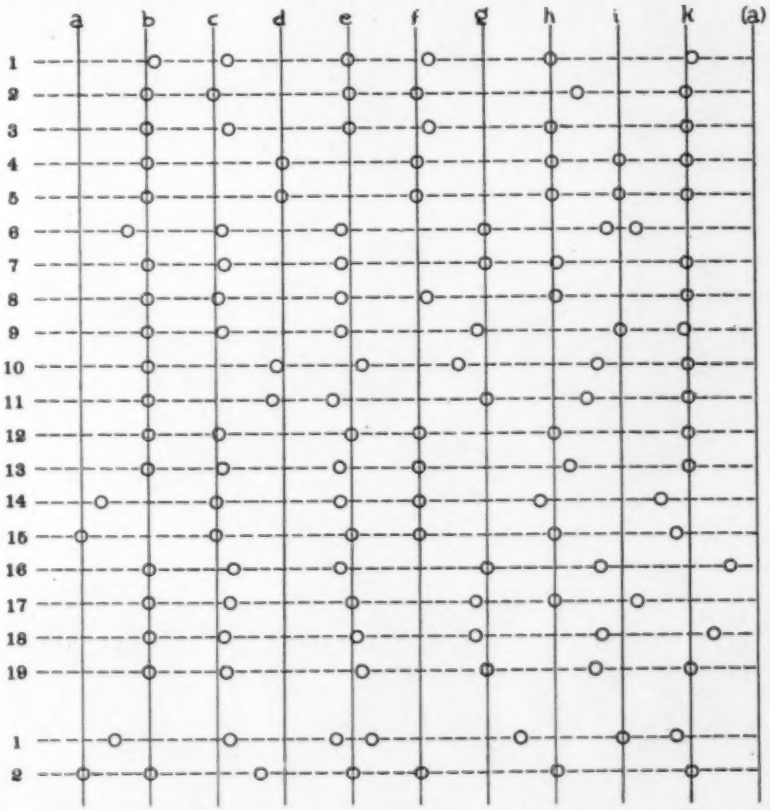
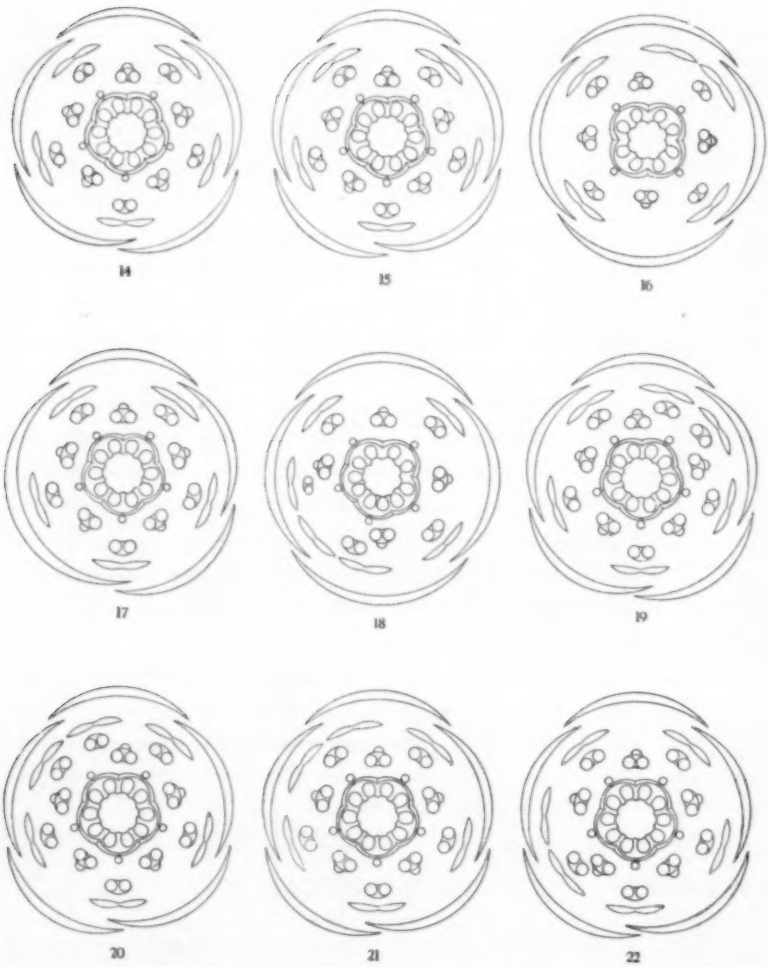
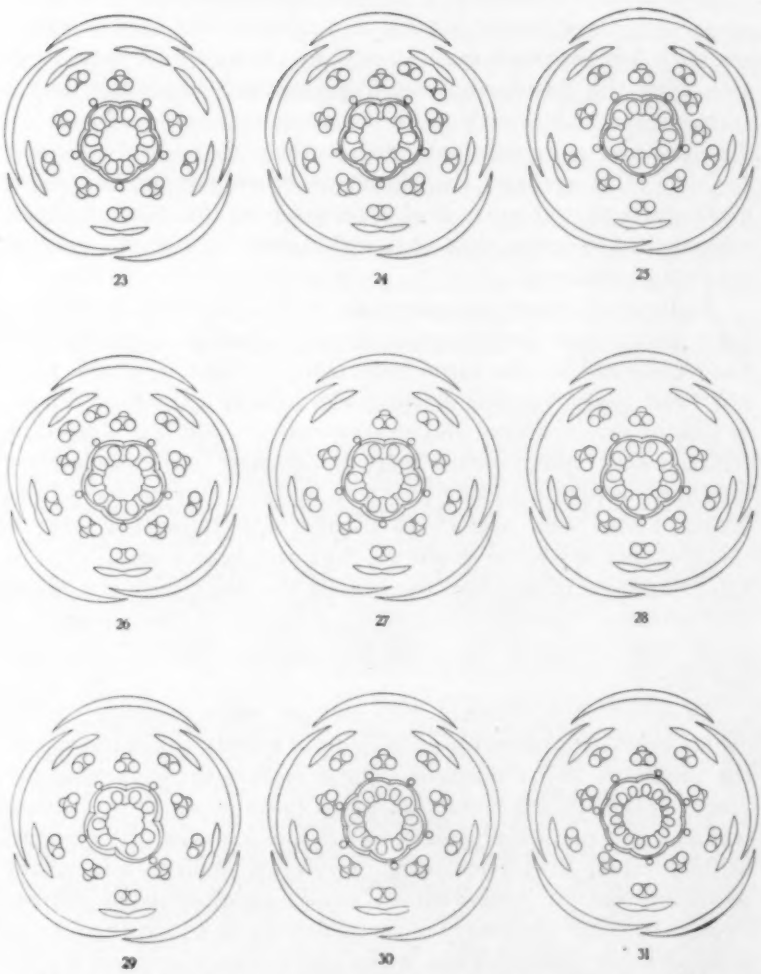


Fig. 13. Position of the styles in 19 six-styled flowers and 2 seven-styled flowers having the sepals overlapping as in figure 7.

The number of stigmas and styles is largely independent of that of the other organs. In only about one-fifth of the total number of flowers with other than five stigmas was one or more of the other whorls irregular. Since the variation in the number of carpels is greater than that of all the other parts



Figs. 14–22. Floral diagrams of *Stellaria aquatica*: 14, 15, typical flowers having the sepals overlapping as in figures 7 and 6 respectively; 16, 17, 18, flowers having four sepals; 19, 20, 21, 22, flowers having six petals, 19, 20, having eleven stamens.



Figs. 23–31. Floral diagrams of *Stellaria aquatica*: 23, a flower having six petals, nine stamens; 24, 25, 26, flowers having 11 stamens in various positions; 27, 28, flowers having nine stamens; 29, a flower having four carpels; 30, a flower having six carpels; 31, a flower having seven carpels.

combined it is evident that they must vary independently. There is a large number of possible combinations in the number of parts in the different whorls, and a great many occur. Flowers with four stigmas may have four, five, or six sepals; so also with the flowers having five stigmas. The number of stamens associated with these parts also varies. A few of the different and more common combinations are shown in figures 16-31. It is realized that here, as elsewhere in this work, mathematical and statistical treatment of the data might be offered, but it seems that that would add little to the general concepts presented.

Individual plants for purposes of flower study have not been grown; but flowers with varying numbers of parts have been observed in the same inflorescence; that is plants have not been found bearing flowers which have only four sepals, or four or six stigmas or eleven stamens etc. While it is possible that one plant may produce more flowers with four stigmas than another, no plants having only the atypical flowers have been found. This also applies to plants with imperfect flowers.

A glance at table 3 shows that the sepals manifest the least variation in number, the carpels the most, with the petals and stamens intermediate. The variability in the number of parts thus increases from the base of the floral axis toward the apex.

In addition to flowers with one or more stamens sterile, others have been observed in which not merely the stamens but the pistils as well are sterile. Such flowers show varying degrees of sterility and reduction, from those in which the petals, stamens and pistil are present but reduced in size, the stamens usually hard, dry, containing shrivelled pollen, the ovary wrinkled, tan or yellowish in color, supplied with minute ovules, to those extremely reduced flowers in which the corolla is apparently missing even when the flower is viewed with a binocular microscope, the stamens very small with little or no pollen, and the pistil very minute or practically failing to develop.

Stellaria aquatica shows two types of sterility, that in which the stamens are in part or wholly non-functional but the pistils produce seeds if pollination is effected, and that in which neither stamens nor pistils function. Flowers of the latter

type may be produced at various places in the inflorescence, the first flower sometimes being so modified. This represents a weakening of the dichotomous cyme (Parkin, 1914). These sterilities would be considered by Stout (1916) as sterility from impotence; in the one case partial impotence involving the stamens, and in the other complete impotence with reference to both kinds of sporophylls. According to the classification of Sirks (1917) there is partial unilateral sterility (of the stamens), total unilateral sterility (of the stamens), and total bilateral sterility (in which both stamens and pistils fail to function). Whether there is a partial and total unilateral sterility involving the pistils has not been determined. These types of sterility are found rather commonly in the angiosperms.

GENERAL CONSIDERATIONS AND DISCUSSION

From the data presented in the preceding pages it is evident that the variations in *S. aquatica* are governed, to an extent at least, as to their position in the flower; by the frequent occurrence of variations in definite positions, axes of symmetry are established, through position *h* with reference to additional petals, three-lobed petals, and additional stamens, through position *f* with reference to missing stamens, through position *a* in flowers having four stigmas, and through position *d* in flowers having six stigmas. These axes are shown in their relationships in figure 5b, the axis through position *h* being indicated with a solid line in each flower, that through *a* and *f* with a broken line, that through *d* with a dotted line. While it is true that the oblique directions of the internodes in the inflorescence cannot be shown in such a diagram, the bracts at the nodes are typically horizontal in the living condition, as are the flowers while they are open, so that except for the different levels in the inflorescence the diagram is representative of the relations as they actually exist. It remains still to be established however that all the axes of symmetry represented there can occur in each of the positions in the inflorescence; this has not been investigated in the present study. As a rule of course not more than one of the axes is established in the same flower. Comparing the two flowers which terminate the two branches originating at the same node in the inflorescence with the flower at that node it is evident that the axis through

f in flower number 2 in figure 5b forms an angle of 90° with the axis through *f* in flower number 1; the axes through *h* in these two flowers also form an angle of 90°, and those through *d* also form the same angle. On the other hand the axis through *f* in flower number 2′ forms an angle of 162° with the axis through *f* in flower number 1, that through *h* in flower number 2′ one of 18°, and that through *d* one of 54° with the similar axes in flower number 1 respectively. Similarly the axes of flower number 3 are at right angles respectively with those of flower number 2, while those of flower number 3′ through *f*, *h*, and *d* again form angles of 162°, 18°, and 54° respectively with the similar axes of flower number 2. The axes of flowers number 3′ and 2′ are again at right angles, while those of flowers number 3 and 2′ again form angles of 162°, 18°, and 54°. It may thus be said that of the two branches developing at a flowering node, that terminated by a flower having the sepals homodromic in origin with those of the flower at the node from which the branch develops will have these axes all at 90° with the similar axes of the flower at that original node; in the flower terminating the other branch these axes through positions *f*, *h*, and *d* will be at angles of 162°, 18°, and 54° respectively with the similar axes of the flower at that original node.

Axes *f*, *h*, and *d* in flower number 2 form angles of 108°, 108°, and 36° with the same axes in flower number 2′; this is true also for flowers 3 and 3′, 4 and 4′, etc., for flowers terminating branches which originate at the same node. It may then be further said that the axes through *f*, *h*, and *d* of the one of two flowers terminating the two branches originating at the same node in the inflorescence will form angles of 108°, 108°, and 36° with the same axes of the flower terminating the other branch. The *f* axes of flowers 1 and 3′, 2 and 4′, 2′ and 4, 3 and 5′, etc., form angles of 108° (or 72°); the *h* axes also form angles of 108° (or 72°); the *d* axes form angles of 36° (or 144°). It is thus possible to consider the relationship between these axes of symmetry even though their occurrence in the inflorescence may not be very frequent. The relationships will usually not be as diagrammatic as in the figure.

It is evident that there are fluctuating variations in *S. aquatica*. The general topic of fluctuating variations has re-

ceived its due share of pages in modern biological literature. Whether evolution is considered to be due to the accumulation of minor variations, or whether the key to the scheme of descent is sought in larger mutations, variations of a minor nature cannot be denied throughout the organic world; it is their interpretation that gives rise to disagreement. Morgan, Sturtevant, Muller, and Bridges (1922) assert that the effects of factors may be modified by 'environmental' and 'developmental' influences as well as by other factors. Morgan (1926) admits the possibility that the gene may be stable 'because it fluctuates quantitatively about a persistent standard', though he inclines to the view that 'the gene is constant because it represents an organic chemical entity.' The importance of the environment, especially as regards sexual relations in plants, has been strongly emphasized by Schaffner (1921, 1922, 1923a, b, 1926, 1927a, b, 1928) whose extended observations and experiments show that in certain plants at least, such as *Cannabis sativa*, *Arisaema triphyllum*, *Arisaema Dracontium*, *Humulus japonicus*, and *Zea Mays*, the important sexual relations may be modified by external influences.

Aside from the importance of variations from the evolutionary and genetic standpoints among others, they are of significance also in the concept of types. This concept is ancient; it goes back at least to Aristotle. With the development of systematic botany, especially by Linnaeus; the nomenclatorial type concept received a great impetus.

While the existence of forms in evolutionary relationship has been so universally admitted since Darwin's time, their boundaries, partly at least because of their variability, have been much disputed. The existence of races and varieties in many species cannot be questioned; and the study and establishment of such varieties can apparently go to great lengths. The present study, however, has not been in the nature of a genetic investigation; such researches are still to be done on *S. aquatica*. That lines could be established, 'pure' for various characteristics at least, seems possible. But these would still have much in common with the conept of *S. aquatica* presented in the preceding pages; and such work would make a previous general study of the plants as found in nature all the more fundamental.

Despite the great number of species, races, and varieties

described for many plants, the concept of biologic types which are the results of physical and chemical forces has not been strongly emphasized. For the lower plants Harper (1916, 1926) has put forth such factors as the angular relations of cells, mutual pressure, adhesion, surface tension, and inherited form tendencies; and again diminishing load and maximal resistance. Lewis (1923, 1925) has established the tetrakaidecahedron as the type for cells in certain tissues.

There has been an attempt in the preceding pages to disclose the type, if any be present, for the stem, the inflorescence, and the flower of *S. aquatica*. In any complete study of types not merely a single species but related forms as well should be investigated. The stem with leaves decussately arranged seems to be typical. Whether the symmetrical production of branches in a single or in a double spiral is to be considered the true type, or whether it is passing from one to the other is still an open question. To say with Thompson (1917) that phyllotaxy is due to the 'steady production of similar growing points, similarly situated, at similar intervals of time' is merely putting the problem one step farther back; and the 'laws' of cell division and growing points are intricate but not unquestioned.

The symmetry of the true dichotomous cyme suggests a real type, and the regular, pentamerous, symmetrical flower is a type in itself. Loss of parts apparently has been and is going on in the stem, the inflorescence and the flower. This may be the explanation of single and double spirals formed by the branches on the stem, especially since the condition of opposite leaves is looked upon as a derivation from an originally spiral type; it undoubtedly seems to be the explanation of the breaking down of portions of the cyme and the reduction in the floral parts. This too, it is realized is by no means an ultimate answer. Whether the production of supernumerary floral parts is a tendency toward type formation in a new direction, or a harking back to an original type with a larger number of floral parts cannot yet be regarded as settled; the latter is in agreement with accepted theories as to the origin of the Caryophyllaceae.

The physical and chemical bases of stability in the higher plants, aside from angular relations and patterns of symmetry are difficult to approach, and further interpretations are reserved for the accumulation of additional data.

In the preceding pages emphasis has been put upon variations as emphasizing the types. The results indicate that many of these minor differences not only in plants of the same species, but even in different parts of the same plant, are not merely haphazard, but in many cases definitely fixed. The ultimate explanation of the possibility of predicting in which position in these terminal, usually actinomorphic flowers certain irregularities will occur with reference to the sepals, and consequently with reference to the bracts, the inflorescence, and the branches of the stem, is still unknown.

SUMMARY

1. Primary stems of *Stellaria aquatica* have the branches, and branches in turn have the smaller branches upon them arranged either in a clockwise or in a counterclockwise spiral, and sometimes in a double spiral. Clockwise and counterclockwise spirals occur in approximately equal numbers. The same plant as a rule shows both types of spirals on different branches with no apparent regularity in their distribution. There may be apparent reversals in the direction of the spirals.

2. The cotyledonary node frequently has two branches in the axil of each leaf, and the two following nodes have as a rule one branch in the axil of each of the leaves.

3. As pointed out by the older authors, the overlapping of the sepals of the first flower is correlated with the arrangement of the branches; the position of the flower in the inflorescence is also correlated with the position and overlapping of the sepals and the direction of the bending of the pedicels as shown diagrammatically in figure 5b.

4. There is a decided variation in the number of parts in the flower, increasing from the base of the floral axis toward its apex, the sepals manifesting the least variation, the carpels the most. Additional petals and stamens, missing stamens and carpels, and probably additional carpels are fairly fixed as to the position in the flower in which they most frequently occur with reference to the sepals, and consequently with reference to the bracts and the position in the inflorescence. Thus axes of symmetry are established in the flower in definite relationship to similar axes in other flowers in the inflorescence.

5. There is a sterility of the stamens which shows a rather

gradual increase as the season progresses. Certain stamens are more frequently sterile than others. Some flowers show sterility of both stamens and pistils, such flowers being comparatively minute.

6. The type characteristic of the stem, the inflorescence, and the flower of *S. aquatica* is emphasized.

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Not Piper angustifolium Lamarck: not Piper elongatum Vahl

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Ever since scientific names have been given to what are taken for species in nature as a means of intelligible reference to them, it has been recognized that one name cannot consistently designate more than one species. By common consent naturalists have come to retain a given name for the species to which it was given first, whenever through lack of information or through error it has been applied to several species. Though constituting no part of the name, an indication of the person who first published it is commonly appended to it; and pending its complete stabilization, it usually is followed by a negative indication of the same name, with similar author citation, in case others have used it to designate other species.

In 1791 Lamarck named a small Cayenne shrub *Piper angustifolium*. So far as known even yet, it occurs only in the Guianas and the lower Amazon region.

Seven years later, apparently in ignorance of Lamarck's publication, Ruiz and Pavon gave the same binomial, *Piper angustifolium*, to the narrower-leaved form of 'matico,' which is confined to the eastern slope of the Andes and is exported, for medicinal use, chiefly from Bolivia. Obviously, *Piper angustifolium* Ruiz and Pavon, not *Piper angustifolium* Lam., needed rechristening; and in 1805 it was renamed *Piper elongatum* by Vahl.

For some reason, possibly through similar oversight, Roxburgh in 1820 again used the same binomial, *Piper angustifolium*, for an entirely different Indian herb; and a decade later Dietrich entirely renamed this *Piper angustifolium* Roxb.,—not *P. angustifolium* Lam., not *P. angustifolium* Ruiz & Pav.,—*Peperomia Roxburghiana*, though he might possibly have done better by retaining the trivial name given by Roxburgh when making the new binomial, as was done by Casimir de Candolle subsequently, under a procedure now generally approved.

Quite paralleling the practice of fixing one binomial for each kind of plant, and an expression of the same effort to give unmistakable significance to names, there has arisen the common practice of bringing together for each species under its accepted name any different names which it may have received through

oversight or error. The elimination of such synonyms borne by a given species is of equal importance with the elimination of all but one species designated by a given homonym.

This conventional treatment of both synonyms and homonyms is essentially a matter of book-keeping, based on ascertained facts. Unfortunately fact and opinion are not always sharply separable in the interpretation of 'species,' and it is quite humanly possible to err either in considering two differently named forms to be specifically identical or in considering two identically named forms to be specifically separable. This is a very weak point in a mid-Victorian convention which considered a binomial duly relegated to synonymy as virtually non-existant and therefore fully applicable to any other species.

That the medicinal 'matico' continues to be spoken of commonly—and uniformly in pharmacal circles—as *Piper angustifolium* Ruiz and Pavon, results from a still prevalent belief that finality in human judgments is achievable. After the Piperaceae had been monographed in 1869 by Casimir de Candolle, such finality was accorded his judgments as those of the only competent authority on a large and most intricately difficult family of plants.

In this classic handling of the genus *Piper*, Lamarck's prior use of the specific name *angustifolium* was not recognized as displacing the more familiar homonym of Ruiz and Pavon, so that the binomial *Piper angustifolium* was adopted for the 'matico'—under it, as synomyms, being placed the name *Piper elongatum* Vahl and its later equivalents *Steffensia elongata* Kunth and *Artanthe elongata* Miquel, as well as *Piper purpurascens* Dietrich; while the monographer forecasts rather than declares the now evident conclusion that what he names *Piper salviaefolium* (*Artanthe salviaefolia* Miquel) is likewise of this species. Published mention of *Piper angustifolium* or *Piper elongatum* from that point on compels recognition that there is fallacy in supposing that affixing an author's name to a binomial at all necessarily shows what the author himself meant when he named a species, because it actually shows only what the later writer considered and intended the accepted name to stand for.

Up to this point, the synonymy of the 'matico' is free from error except that Vahl's binomial should have headed the

list and that the name used by Ruiz and Pavon should have replaced it in the list of synomymic discards. Unfortunately a graver error enters here, because the geographically localized 'matico'—which has deeply bullulate-lacunose leaves—was not distinguished from a somewhat similar Peruvian pepper with smoother leaves that Ruiz and Pavon themselves had named *Piper granulosum;* and either directly or as varieties this and several similar forms were made to extend the range of the amplified *P. angustifolium* as far afield as through Brazil to the east and Panama and Cuba to the north.

Fuller and better and more extensive collections now make it certain that these outlying forms and the Peruvian *P. granulosum* are not co-specific with *Piper elongatum* or *P. angustifolium* in the sense intended by Vahl or Ruiz and Pavon, and they are very different from *P. angustifolium* Lam. These plants constitute a natural group and resemble *P. elongatum* chiefly in having hooked or strongly curved aments. From one another they differ in geographic occurrence, but their morphologic differentials are not readily stated with positiveness in every case.

The prototype of these outlying 'angustifolium' or 'elongatum' forms is the Jamaican *Piper aduncum* Linnaeus (1753), under which some of them have been put as forms of late years and in which all should be included if they represent a single species. The next in priority is the Peruvian *Piper granulosum* Ruiz and Pavon (1798), followed successively by the Venezuelan *P. celtidifolium* Kunth (1815), the Mexican *P. multinervium* Martens and Galeotti (1843), and the Caribbean *P. subrectinerve* C. de Candolle (1902).

If these are to be kept apart, as in my present opinion they should be, *P. granulosum* Ruiz and Pavon is limited to the southern Andes; *P. celtidifolium* Kunth ranges from the Colombian-Venezuelan region through the Isthmus and as far north in Central America as Nicaragua; *P. multinervium* Martens and Galeotti continues the series from Salvador to Mexico; and *P. subrectinerve* C. DC. is the Caribbean representative of *P. aduncum* Linnaeus, which, when these are excluded, is confined to the Greater Antilles, where it is accompanied by a very hairy form, *P. Ossanun* (C. DC.) Trelease.

The vastly diversified countries embracing the extensive lowlands east of the Andes also have *aduncum*-like peppers, some of which have received separate names; but none of them is capable of affecting the designation of the more boreal forms, whether these be kept apart, merged into one, or united in part only.

Still another use of the binomial *Piper elongatum* presents other and different nomenclatorial difficulties. Under the then fully sanctioned practice of re-employing in a quite new sense a name which had been buried in synonymy, Monsieur de Candolle did not hesitate to make use in the Prodromus of this discarded name for a Brazilian plant of the palmately nerved Enckea group (all of the other '*elongatum*' forms being pinnately nerved Artanthes).

Though Monsieur de Candolle's riper study, embodied in a 'Piperacearum Clavis' on which his latest years were spent and which was published after his death, was not cast in a form specifically showing such facts, he rehabilitates in the 'Clavis' the true *Piper angustifolium* (though an error of the indexer of the work ascribes the name to Ruiz and Pavon instead of Lamarck), and he properly takes up for the 'matico' Vahl's name *Piper elongatum*—though unfortunately in the complicated sense in which it was understood when called *angustifolium* in the Prodromus sixty years ago.

Unfortunately, though his earlier re-employment of *elongatum* when the name was supposedly dead is set right in the 'Clavis' by renaming the Brazilian Enckea *Piper hexandrum*, the converse untenable rechristening of Lamarck's *angustifolium* as *Piper consanguineum* (the trivial name adopted from Kunth) escaped correction when the 'Clavis' was prepared. It may be added that the Cayenne component of *P. Schlechtendahlianum* of the Prodromus is a co-type of Lamarck's species.

The purpose of this short negative contribution is not to clear up with finality the nomenclature of all of the species which at one time or another have been called *Piper angustifolium* or *Piper elongatum*, but to present positively the fact that neither of these names is applicable to any known pepper occurring in the West Indies or on continental North America.

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Notes on Fabaceae—XII

PER AXEL RYDBERG

ASTRAGALUS L.

The genus *Astragalus* dates back to Linnaeus' Species Plantarum, where the author adopted it from Tournefort and other older writers. In fact it dates back to the old Greeks, who used the name for some leguminous plant. The historical type is probably *Astragalus christianus*, but *A. Onobrychis* L. should be regarded as the nomenclatorial type according to the American Code. It should therefore be limited to species with a two-celled, more or less woody, bony, or leathery, and short and sessile pod. These requirements are fulfilled by the sections ONOBRYCHIDES, ULIGINOSI, MOLLISSIMI, and CHAETODONTES of Gray's, Watson's, and Jones' revisions of the genus. I have also included *A. lentiformis* and *A. Lemmonii*, though the pod is reflexed, rather thin-walled, and acute on both structures, and *A. Breweri*, which Gray placed in the section OROBOIDEI and Jones in his DIDYMOCARPI. In Europe and Asia, the genus, as so limited, is represented by numerous species.

1. MOLLISSIMI

1. ASTRAGALUS GIGANTEUS S. Wats. was described from fruiting specimens collected by Dr. Havard at Fort Davis, Texas. Sheldon changed the name to *A. texensis* on account of the earlier *A. alpinus giganteus*. M. E. Jones regards it as the same as *A. yaquianus* S. Wats., and his description applies mainly to this. In my mind the identification is not well established, for *A. giganteus* is described as having 5 to 10 pairs of villous-pubescent leaflets and *A. yaquianus* as having 10–21 pairs of appressed villous leaflets. The type specimen of the former is much more hairy than in *A. yaquianus*. Jones (Rev. Astragalus 234. 1923) makes the following statement: 'Pringle's No. 1218 distributed as a part of the type of *yapuianus* [*yaquianus*] is this species.' This is not quite correct, for the latter was *wholly* based on that number. Jones, notwithstanding, proposes a new variety, *A. giganteus* var. *yaquianus*, based on Watson's species as to the name, but the description applies to the next species. Jones also gives the distribution as extending to Guerrero. This is not, as it seems, the state of

Guerrero, but the type locality of *A. yaquianus* on the Yaqui River which was near the town of Guerrero, Chihuahua. It is related to *A. mollissimus*, but has better developed stems, ochroleucous flowers, nearly straight, abruptly acuminate, and broader pod. The following specimens belong to *A. yaquianus*:

CHIHUAHUA: Upper Yaqui River, *Pringle 1218;* Madera, *Palmer 295.* —NEW MEXICO: Lincoln County, *Wooton* in 1895; *3423* in 1907, *3960* in 1908; *Plummer* 1903; *Eggleston 14446, 14452;* White Mountains, *Wooton 327;* Gray's Peak, *Earle & Earle* in 1900; Ruidoso Creek, *Wooton* in 1895; Lincoln County, *Eggleston 14446.*—TEXAS: Upper Concho, *Reverchon 1281;* Fort Davis, *Havard; Ferris & Duncan 2543.*

2. ASTRAGALUS HARTMANII Rydb. See notes under the preceding species, from which this differs in the much larger flowers and large, thin, and less pubescent leaflets. It is known only from the type locality, San Diego Ranch, Chihuahua, *Hartman 678.*

3. ASTRAGALUS MOLLISSIMUS Torrey was described from specimens collected by James on the Platte River. Together with the two preceding, it differs from the rest of the species of the group by the glabrous pod. Jones made the following statement that the pod is 'inclined to be velvety pubescent when young,' which I think is wholly erroneous. In New Mexico the plant is often much smaller than on the plains, with smaller leaflets, flowers, and fruit (*A. simulans* Cockerell). Such specimens are:

NEW MEXICO: *Wright 367;* Las Vegas, *Cockerell* in 1901; Gray, *Skehan 7;* Roswell, *Tinsley*, in 1899; Union Co., *Standley 6122.* —Texas: Estelline, *Reverchon 4297.* The distribution of the species extends from Nebraska and Wyoming to Texas and New Mexico. Jones reported it from Flagstaff, Arizona, but I doubt the record.

4. ASTRAGALUS ORTHANTHUS A. Gray resembles *A. yaquianus* and *A. Hartmanii* in the more or less elongated stem, in the large flowers, and the straight banner, but the color of the flower is more red, or in one form white, the pod more rounded and densely pubescent.

VERACRUZ: Perote, *Halstead* (type).—NUEVO LEÓN: Saltillo, *Palmer 2137* (?).—PUEBLA: between Tinguattan and Cerro León, *Liebman 4683.*

5. ASTRAGALUS SANGUINEUS Rydb. It is related to *A. orthanthus*, but the plant is merely strigose, and the pod is larger and rounded at each end. The pod illustrated by Jones as *A. orthanthus* (Rev. Astragalus *pl. 60, fig. 195*) belongs to this species.

NUEVO LEÓN: Saltillo, in 1880, *E. Palmer 243* (U. S. Nat. Herb. *43559*).

6. ASTRAGALUS HUMBOLDTII A. Gray was based on *Phaca mollis* H. B. K., the type of which came from Gasove, Valley of Mexico. Dr. Gray cited only one specimen that he had seen, viz. one in the Torrey Herbarium collected by Halstead, near the City of Mexico. Humboldt's specimens according to *Nova Genera et Species* were without fruit, and so is Halstead's, but both the original description of *P. mollis* and the plate, as well as Halstead's specimen, agree well with the species of southern Mexico, that is, with *A. Orizabae* Seaton, which name becomes a synonym. The plant of northern Mexico which has gone under the name of *A. Humboldtii* is quite different, and was until lately evidently without a published name. To *A. Humboldtii* belong the following specimens.

MEXICO (Federal District and State): *Humboldt; Halstead; Pringle 7137, 11953;* Irola, *Rose & Hough 4557*, in part.—VERACRUZ: Orizaba, *Seaton 262; Mueller* in 1855; *E. W. Nelson 282.*—PUEBLA: *Arsène 1600; 7102;* Chalchicomula, *Pringle 8565; Rose & Hay 5663;* Esperanza, *Pittier 403; Purpus 3051.*—HIDALGO: Pachuca, *Purpus 401; Rose, Painter & Rose 8810;* Tequizquiac, *Rose & Painter 6635.*—QUERETARO: Between Cadereyta and Visaron, *Rose, Painter & Rose 9756; Altamirano 1645.*

7. ASTRAGALUS EARLEI Greene. The first reference to this species may be found in Biologia Centrali-Americana, where Hemsley cites under *Astragalus Humboldtii* a specimen collected by Potts in Chihuahua, the true *A. Humboldtii* not being found in northern Mexico. The specimens distributed from there and so labelled belong mostly to the present species. It may be that Jones had derived his concept of *A. Humboldtii* from such specimens as *Pringle 883*, when he drew his description. The species is intermediate between *A. Bigelowii* and *A. Humboldtii*, perhaps nearer the former, differing in the more elongate, more curved pod, with much shorter hairs, the corolla also being smaller. As Jones cited no specimens, though

he gave a good description of this species, I adopted an unpublished name of Dr. Greene's and assign as the type *Earle & Tracy* (or *Tracy & Earle*[1]) *226* as the type. Greene has also assigned another name to another number of the same collection.

TEXAS: Limpia Cañon, *Earle & Tracy 226* (type, N. Y. Bot. Gard.); *237; 221; 276;* Davis Mountains, *331; Ferris & Duncan 2661;* Marfa, *H. C. Hanson 389;* Fort Davis, *Eggleston 20201.*—NEW MEXICO: Las Vegas, *Anect 40.*—CHIHUAHUA: Vicinity of the City, *Pringle 189, 883; Palmer 5,* and *78,* in 1908; Parras, *Palmer 242;* Saltillo, *Palmer 241.*

8. ASTRAGALUS IROLANUS (M. E. Jones) Rydb. This is closely related to the preceding, differing mainly in the acute leaflets and the large flowers.

HIDALGO: Irola, *Rose & Hough 4557,* in part; (type)—MEXICO (State): Ixtapalapa, *Rose & Hay 5641.*

9. ASTRAGALUS PERVELUTINUS Rydb. The type was distributed as *A. Humboldtii.* It is related to it, but the pod is not so much inflated, slightly curved and more densely hairy. From *A. Earlei* it differs in the broader, less curved pod, and the larger flowers, and from both in the short tangled pubescence of the leaves, the broader leaflets densely covered with short tangled hairs.

CHIHUAHUA: City of Chihuahua, *Pringle 189* (type in herb. N. Y. Bot. Gard.)—DURANGO: Tepehuanes, *Palmer 14.*

10. ASTRAGALUS BIGELOWII A. Gray is closely related to *A. mollissimus,* but differs mainly in the densely pubescent, broader and shorter, less arcuate fruit. The pubescence is also usually looser and the leaflets more round. It is distributed from Texas to Arizona, Durango, and San Luis Potosí.

11. ASTRAGALUS THOMPSONAE S. Wats. was described from specimens collected by Mrs. Thompson in southern Utah and named for her. Sheldon changed the name to *Astragalus syrticolus* on account of the older *A. Thompsonianus* Benth. Jones regarded it as a variety of *A. Bigelowii,* but it is readily distinguished by the white, short, and more spreading pubescence, the lax recemes, and the larger and different pod. It is common in eastern and southern Utah; it has also been collected elsewhere, namely:

[1] It has been distributed both ways.

ARIZONA: Deadman Ranger Station, Coconimo County, *Eggleston 17189;* Moki Reservation, *Hough 56.*—NEW MEXICO: Aztec, *Baker 405.* —COLORADO: Westwater, *Jones,* in 1891; Mesa County, *H. C. Long,* in 1893.

12. ASTRAGALUS MATTHEWSII S. Wats. is related to *A. Bigelowii* and *A. Thompsonae,* but differs from the former in the white pubescence, the larger, less arcuate, more inflated and more long-hairy pod, the upper suture of which is almost straight, and from the latter in the more appressed pubescence and the less curved pod. It is known only from the type collection, from Fort Wingate, New Mexico, by Dr. Matthews, and by Dr. Palmer without locality.

13. ASTRAGALUS MOGOLLONICUS Greene is also related to *A. Bigelowii* and by Jones regarded as identical with it. The type, however, is covered with a long, brown, spreading pubescence, the raceme is nearly capitate and very dense, the leaflets suborbicular and the pod, sent later by Dr. Greene, is very small, about 1 cm. long, 5 mm. broad and deep, white-villous, scarcely sulcate on either suture and straight on the upper. It is known only from the type collection, Mogollon Mountains, New Mexico.

14. ASTRAGALUS MARCIDUS Greene is related to *A. Bigelowii* but the flowers are much smaller, the pod smaller and nearly straight on the upper suture.

TEXAS: Davis Mountains, *Tracy & Earle 319* (type); Marfa, *C. B. Greene* in 1895.—CHIHUAHUA: San Diego, *Hartman 605.*—COAHUILA: Aqua Nueva, Saltillo, *Palmer 559.*

15. ASTRAGALUS ANISUS M. E. Jones. This was collected near Pueblo, Colorado, by Miss A. P. Lansing in 1888, and evidently has never been collected since. It is not closely related to the other spieces of the group, differing from the rest in the small size, the appressed silky pubescence, the comparatively small flowers, and in the pod, which is more rounded, merely mucronate, more inflated, and with short appressed pubescence. Only *A. Matthewsii* approaches it in the pubescence of the leaves, and *A. Humboldtii* in the shape of the pod. In the National Herbarium there is a specimen somewhat similar without collector's name. The only original record given is 'Camp 82–83 April 28.' Dr. Gray has written on the label 'Apparently *Astragalus succumbens* Dougl.,' which evidently is wrong.

2. ULIGINOSI

16. ASTRAGALUS CAROLINIANUS L. This species was based on a description and plate in Dillenius' Hortus Elthalmensis. Most botanists have regarded this as the same as *A. canadensis* L., and the name has place priority on the page. Dillenius' plate resembles more the common plant here regarded as *A. canadensis*. Appended to his description, however, there appeared a comparison between *A. carolinianus* and another species on which Linnaeus based his *A. canadensis*. The only clue on which to base the identification of the latter is given in the description of the leaflets, which are said to be subcanescent beneath. This could only apply to the northern and more common plant, for in the southern plant the leaflets are sparingly and minutely strigose beneath. In the figure the calyx teeth are illustrated as very short, while in fact they are in *A. carolinianus*, as here understood, longer than those of *A. canadensis*, but this may have depended on the inaccuracy of the artist. As there are two closely related plants in eastern United States, and the northern one has the leaves subcanescent beneath, it may be well to retain the name *A. canadensis* L. for this, and reserve the name *A. carolinianus* L. for the southern. Jones regarded the latter a variety of the former, but his description of the pod 'decidedly inflated' is erroneous, for the pods are alike in both species, being oblong, not sulcate, and perfectly glabrous. Perhaps he confused it with *Phaca neglecta*.

MARYLAND: Cumberland, *Schriver* in 1874.—VIRGINIA: Bushy Mountain, Smyth County, *Small* in 1892; Luray, *Steele & Steele 46;* Wytheville, *Shriver* in 1874.—WEST VIRGINIA: Hinton, *Millspaugh 1146;* White Sulphur Springs, *A. Brown* in 1892.—NORTH CAROLINA: Table Rock, *Heller 32;* Great Smoky Mountains, *Beardslee & Kofoid* in 1891; Yellow Hill, Swain Co., and Balsam Mountain, *Hulst* in 1882.—GEORGIA: Tugalo River near its junction with Seneca, *Gibbs* in 1855.

17. ASTRAGALUS CANADENSIS L. See notes under the preceding species. This is the most widely distributed species of *Astragalus* in North America, its range extending from Quebec to Hudson Bay, Alberta, Utah, Colorado, Oklahoma, and Virginia. There is also a record from Kettle River, British Columbia, *Macoun 63754* and one from Dallas, Texas, *Reverchon*.

18. ASTRAGALUS HALEI Rydb. The type was collected in Louisiana, *Dr. Hale 313* (Torrey Herbarium, flowers); also at Shreveport, *Cocks 3624* (fruit). It is closely related to *A. carolinianus* but has about half as long calyx-teeth, and spreading fruit.

19. ASTRAGALUS OREOPHILUS Rydb. The type of this species came from Pagosa Spring, Colorado. It is intermediate between *A. canadensis* L. and *A. spicatus* Nutt., differs from the former in the usually broader leaflets, the broader and shorter bracts, the flowers more resembling *A. spicatus* and the plumper pod, and from the latter in the glabrous, less coriaceous pod and the narrow upper calyx-lobes.

COLARADO: Walsenberg, *Shear 4769;* Pagosa Springs, *Baker 419* (type); Trimble Springs near Durango, *Baker, Earle, & Tracy 478;* Wahatoya Creek, *Rydberg & Vreeland 5990;* Larimer County, *Osterhout* in 1897; Boulder, *Tweedy 5154;* Fort Collins, *Crandall* in 1898.—NEW MEXICO: Pecos River National Forest, *Standley 4377;* Colfax, *14656, 13861;* El Vado, Chama River, *Eggleston 5988;* Chama, *Standley 6546.*

20. ASTRAGALUS MORTONI Nutt. The type was collected by Wyeth on the sources of the Missouri. In the isotype in the Torrey Herbarium the specimen in flower has a decidedly black-hairy calyx, and bracts and the ovary is described as villous. Nuttall described the flowers as ochroleucous. Torrey and Gray placed it among the purple-flowered species, between *A. adsurgens* and *A. striatus*, not noticing that the relationship was to *A. canadensis* L., and *A. spicatus* Nutt. Watson made it a variety of *A. canadensis*. Neither Watson nor Jones have noticed that *A. Mortoni* has more or less black-hairy calyx and bracts, nor does the latter make any reference to the fact that the pod in *A. Mortoni* is pubescent and sulcate on the lower suture. In *A. canadensis* it is glabrous and without a sulcus. Both authors confused it with *A. spicatus* Nutt., which has white-hairy calyx. Whether the color of the hairs is of any value is perhaps questionable, but the black-hairy plant seems to be limited to the northwest, west of the continental divide, while the white hairy form is confined to the Rocky Mountains, on the western slope of which their ranges, however, overlap. In the white-hairy plant the pod is less turgid, the upper calyx-lobes are always twice as broad as the rest, and the bracts

broad and short. In the true *A. Mortoni*, the bracts and even the calyx-lobes approach more those of *A. canadensis*, but are shorter, and the pod less hairy and with a straighter beak than in the white-hairy plant, and sometimes glabrate in age. It is confined to the Pacific slope and widely distributed in Washington, Oregon, Idaho, northern California, and western Montana. It has been collected east of the Rocky Mountains at the following stations.

MONTANA: Helena, *Butler 104, 1042;* Gannet, *Mrs. Scheuber* in 1901. —WYOMING: Gros Ventre River, *Merrill & Wilcox 994.*

21. ASTRAGALUS PACHYSTACHYS Rydb. This species was based on *Astragalus spicatus* Nutt.; not *A. spicatus* Pallas. See notes under *A. Mortoni*. Both Watson and Jones included this in *A. canadensis Mortoni*. The type came from the Rocky Mountains, most likely Wyoming. *Astragalus tristis* Nutt., which has also been regarded as a synonym of *A. Mortoni*, might seem to belong here, as the type locality was 'Rocky Mountains, towards the sources of the Platte,' hence Wyoming, but the calyx is described as being black-hairy. The species is unknown to me, as no specimens have been seen. *A. pachystachys* is common in the Rocky Mountains of Montana and Wyoming, especially east of the divide. Besides, the following specimens, found outside of the range proper may be included in it.

IDAHO: Tikura, Blaine County, *Nelson & Macbride 1293;* Bear Lake County, *1617;* Blackfoot, *Mulford;* Lake Waha, *Heller 3089;* Latah Co., *Sandberg;* Pocatello, *Mrs. Soth 544.*—WASHINGTON: *Vasey 275;* Wilson Creek, *Lake & Hull 667;* Simcoe Valley, *Lyall;* Egbert Spring, *Sandberg & Leiberg;* Brickelton, *Suksdorf 2268;* Newman Lake, *8803.*—BRITISH COLUMBIA: Lake Osoyoos, *Macoun 70438.*—NEVADA: East Humboldt Mountains, *Heller 9204; Watson 261,* in part.—SOUTH DAKOTA: Black Hills, *Forwood; Murdock.*

22. ASTRAGALUS TORREYI Rydb. The plant was first collected by Torrey and in the same year by Stretch. The latter specimen was named by Torrey as *A. adsurgens*. So were also Kennedy's specimens. *Heller 9465* and *9822* bore the name *A. nitidus*, which practically meant the same. I suppose that this misidentification depended on the fact that the leaflets are decidedly pubescent on the upper surface. The rest were

named *A. Mortoni*, but the calyx is not black-hairy and the pod is more like that of *A. pachystachys*, of which it may only be a form; the leaflets, however, are narrower, the flowers smaller, the calyx-lobes shorter, and the bracts and even the stipules narrower.

NEVADA: Empire City, Nevada, in 1865, *Torrey* (type, herb. Columbia University and N. Y. Bot. Gard.); Ruby Valley near Cave Creek Post Office, *Heller 9465;* Carson City, *Jones 3843;* Pleasant Valley, *Stretch* in 1865; Lake Tahoe, *Kennedy 966;* Carson, *Steinmetz A.*—CALIFORNIA: Lake Tahoe. *Leiberg 5328;* Truckee, *Sonne* in 1888; Mono Lake, *Congdon.*—IDAHO: *Henderson 3298.*

The following may also be referred here, though the leaves are only slightly pubescent above when young.

NEVADA: Carson City, *Heller 9822; Baker 1063.*—CALIFORNIA: Truckee, *Heller 7035;* Summit, *12904.*

23. ASTRAGALUS OREGANUS Nutt. The type came from the 'plains of the Rocky Mountain range towards the sources of the Oregon,' i.e. somewhere in Wyoming or Idaho. The species was described from specimens in flowers only, and the plant was practically lost. Torrey and Gray placed it near to *A. flavus*, probably on account of its ochroleucous flowers and connate stipules. Gray retained it in the same place, including it in his Ocreati. When it was rediscovered by Parry on the Jones' Expedition to the Yellowstone Park, Gray and Watson did not recognize it, but it was redescribed as *A. ventorum* and placed in the section ONOBRYCHIDES, also known as HYPOGLOTTIDES. Jones has transferred it to the ULIGINOSI, which somewhat improved the matter, but it is not very closely related to *A. canadensis* and its relatives, and perhaps should constitute a section by itself. The only specimens in fruit seen by me are *A. Nelson 9427* collected in 1910.

WYOMING: Tough Creek, *Aven Nelson 9427;* Steamboat Mountain, Sweetwater County, *7051;* Point of Rocks, *Merrill & Wilcox 731.*—IDAHO or WYOMING: *Nuttall* (type).

3. HYPOGLOTTIDES

24. ASTRAGALUS STRIATUS Nutt. This was published in Torrey and Gray's *Flora* and was based on *A. Laxmanni* of Nuttall's, *Genera*, the type of which came from 'the hills of Missouri', probably South Dakota. *A. adsurgens robustior*

Hooker is also cited as a synonym, though Nuttall, both in the Genera and in Torrey & Gray's *Flora*, describes the calyx as 'blackish and puberulent' or as 'clothed with short black hairs,' while Hooker describes his variety as white-pilose, with very few black hairs. Hooker called the black-hairy form *A. adsurgens*, confusing it with the Asiatic species. Jones has adopted the name *A. nitidus* Douglas for this species, citing Hooker's *Flora* (1:149. 1834) as the place of publication, a nomenclatorial absurdity, which can not be admitted. For the first, *A. nitidus* Dougl. is not published, merely cited as a synonym of *A. adsurgens robustior*, not of *A. adsurgens* as understood by Hooker. The citation of a manuscript name as a synonym is not publication, either under the American or the International Code, and the name was applied by Jones to the wrong form. In the Torrey Herbarium there are two sheets received from Hooker. One of these sheets is labelled: 'Astragalus adsurgens, Pall. Ex herb Hook. Saskatchewan, Douglas.' This represents the ordinary small plant having the calyx with rather numerous short black hairs. The other sheet bears only 'A. adsurgens β Hook.' without any indication of collector or locality. This sheet contains two larger specimens on which the calyx is almost destitute of black hairs. If this sheet represents *A. adsurgens* β Hook., it is an isotype of *A. nitidus* Dougl. It is, however, not exactly *A. striatus*, for that is the more or less black-hairy common form, usually known in this country as *A. adsurgens*. Neither is it *A. sulphurescens* Rydb., nor *A. Chandonetii* Lunell, which Jones also cited as synonyms of the variety. *A. striatus* Nutt. is so common in the Rocky Mountain region that no specimens need to be cited.

In regard to *A. nitidus robustior* M. E. Jones (Rev. Astragalus 170. 1923) it may be said, that it is a great mixture of facts and errors. It is based on *A. adsurgens robustior* Hooker with *A. striatus* Nutt., *A. sulphurescens* Rydb., and *A. Chandonnetii* Lunell given as synonyms, and the following description: 'Flowers white in short heads, on elongated peduncles. Calyx teeth long.' As stated before, *A. adsurgens robustior* is the basis of *A. nitidus*. *A. striatus* Nutt. is the same as *A. adsurgens* Hook. or *A. nitidus* as understood by Jones, but not of Hooker. 'Flowers white' agrees with the description of *A. Chandonnetii*,

scarcely with that of *A. sulphurescens*, and certainly not with either var. *robustior* Hook. or *A. striatus* Nutt. 'Short heads on elongated peduncles' applies to all, at least in flowering stage; 'calyx-teeth long' only to *A. sulphurescens*.

Astragalus terminalis Wats. in the original publication was said to be related to '*A. adsurgens*,' i.e. *A. striatus* Nutt. It being at that time practically unknown to me, I included it in the HYPOGLOTTIDES in my *Flora of the Rocky Mountains*. Jones has shown its relationship to his own *A. reventoides*, making the latter a variety of the former. I think that they are identical, and that Watson committed an error in describing the corolla as purplish, while in reality it is cream-colored with the keel purple-tipped.

25. ASTRAGALUS CHANDONNETII Lunell. This was first described as *A. adsurgens albiflorus* in 1905 by Blankinship from Montana. As there is an *A. albiflorus* Gand. 1902, the later name of Lunell's has to be adopted. *A. Chandonnetii* differs from *A. striatus* not only in the color of the corolla (rather cream-colored than white as described), but also in the foliage which is densely silky strigose on both sides. In my *Flora of the Rocky Mountains* it was included in the next species.

MINNESOTA: McHugh, near Detroit, *Chandonneti*.—MONTANA: Mount Helena, *Butler 1080;* Mount Ascension, *881, 4079, 1082;* Prickly Pear Valley, *4111;* Deer Lodge, *Rydberg 2699;* Helena, *Kelsey* in 1892; Belt River, *F. W. Anderson* in 1883; *Safford 557*.—WYOMING: Gillette, *E. V. Wilcox 429;* Slater, *Goodding 1737*.

26. ASTRAGALUS SULPHURESCENS Rydb. was described in 1901 from specimens from Georgeton, Colorado. It differs from *A. striatus* in the ochroleucous corolla and the longer calyx-lobes, and from *A. Chandonnetii* in the longer calyx-lobes, the more or less black-hairy calyx and pod, and the glabrous or glabrate upper surface of the leaves. It was redescribed the following year by Gandoger under the name *A. Crandallii*. It is confined to the mountains of Colorado.

COLORADO: Along Platte River, *Jones 851;* Boulder Cañon, *Penard 184;* Boulder, *Hanson* in 1920; Georgetown, *Rydberg* in 1895; *Shear 4509;* Estes Park, *Osterhout* in 1895, and *2806*, 1903; Boulder, *Tweedy 5152; Vestal* in 1913; Empire, *5641;* Como, *Crandall 90; Crandall & Cowen 128;* Clear Creek,

Patterson 18; Eldorado Springs, *Clokey 2809;* Boulder County, *C. P. Smith 3147;* Headwaters of Clear Creek, *Hall & Harbor 136.*—WYOMING: West of Cheyenne, *Morris* in 1901.

27. ASTRAGALUS BREVIDENS Rydb. The type was collected 3 miles north of Whitney, Baker County, Oregon, Febr. 22, 1921., *M. Peck 10360.* The specimens were labeled *Astragalus Mortoni* Nutt., to which it has only superficial resemblance. It is evidently related to *A. Chandonnetii*, but differs in the broader leaflets, glabrous above, the short-villous instead of strigose pubescence on the calyx and pod, and the short calyx-teeth.

28. ASTRAGALUS GONIATUS Nutt. This was apparently first collected by Richardson and then certainly by Drummond and referred to the European *A. hypoglottis.* The American plant was first recognized as distinct in Torrey & Gray's *Flora*, where it was published as *A. hypoglottis polyspermus* (T. & G. Fl. N. Am. **1**: 328. 1838). On the second page following, it was redescribed as *A. goniatus* Nutt.; neither Nuttall, nor Torrey and Gray noted that they were the same species. Jones (Proc. Calif. Acad. II. **5**: 646. 1895), adopting the name *A. agrestis* Dougl., made the same error as he did in adopting *A. nitidus* Dougl., in applying Douglas' manuscript name, cited as a synonym under the variety β, to the species itself. *A. agrestis* in Hooker's *Flora* appears only as a synonym and therefore was not published. Furthermore *A. hypoglottis* of Hooker's *Flora*, of which *A. agrestis* Dougl. is a synonym, is not the plant described by Jones, but a closely related plant with pale caylx, practically devoid of black hairs, long calyx-teeth, about as long as the tube and larger corollas. Douglas' type, or at least an isotype of the same, was seen by me, when visiting Kew and the British Museum in 1901. *A. goniatus* is common in the Rocky Mountain region, extending into eastern Washington and Oregon, and in the northern Sierra Nevada. The following specimens have been collected on the eastern plains.

NEBRASKA: Gordon, *Bates 582.*—SOUTH DAKOTA: Sheep Mountains, *Visher 2391;* Brookings, *T. A. Williams;* Daland, Spink County, *Carter* in 1897; Upper Missouri, *Nicollet.*—NORTH DAKOTA: Leeds, *Lunell* in 1902–6. —MINNESOTA: Fish Lake, *Chandonneti;* Fergus Falls, *Sheldon* in 1892. —MANITOBA: Portage la Prairie, *Macoun & Herriot 70492.*

29. ASTRAGALUS VIRGULTULUS Sheldon was described in 1894 from specimens from Boulder, Colorado, collected by Patterson. It was also noted by Prof. Aven Nelson in his First Report on the Flora of Wyoming without a name, but was distributed as *A. hypoglottis ochroleucus*. Later it was described by Osterhout as *A. hypoglottis bracteatus*. Jones (Proc. Calif. Acad. II. **5**: 647. 1895) first stated that '*A. virgultulus* is the same as *A. agrestis* apparently;' later (Contr. W. Bot. **10**: 65. 1902) as *A. agrestis polyspermus* M. E. Jones, based on *A. hypoglottis polyspermus* T. & G., and at last (Rev. Astragalus 171. 1922) the same, adding that it 'is the form growing unsupported by other plants in more exposed places and is ashy-puberulent with pods 7 mm. long and short internodes.' Sheldon describes it as having ochroleucous flowers, leaflets glabrous above with scattered hairs beneath, calyx-tube slightly pubescent with white hairs, calyx-lobes equalling the tube in length, and pod 10–12 mm. *A. hypoglottis polyspermus* was described as dwarfish and much branched, somewhat decumbent, pubescent, calyx longer than the bracts, very hirsute, the hairs partly black, the teeth scarcely half as long as the tube. As no mention is made of the color of the flower, it is presumed that the color was as described under *A. hypoglottis* i.e. bright purple. In the Nuttallian specimens in the Torrey Herbarium they evidently had been so in the fresh state. Do these descriptions agree? Can any one rely on such statements of identification made by Jones? Sheldon did not describe the large bracts, noticed by Osterhout, but he described the large stipules, which usually accompany the large bracts in this species.

COLORADO: Boulder, *Patterson*.—WYOMING: Laramie River near Colorado Line, *Osterhout* in 1896 and in 1898; Meadow Creek, *A. Nelson 775;* Bitter Creek, *4783;* Elk Mountains *4091*.

30. ASTRAGALUS TARLETONIS Rydberg is also related to *A. goniatus*, but has larger flowers, rather fleshy bracts, and long calyx-teeth as *A. agrestis*, but the calyx is strongly black-hairy. The type came from Five Finger Rapids, Yukon. In the Torrey Herbarium there is a specimen from artic America sent by Dr. Hooker, but without locality or collector. This might have been collected by Richardson. Two specimens

similar to that in the Torrey herparium were found at the Philadelphia Academy. These came through Short's herbarium and are labeled 'Astragalus Hypoglottis, Frankl. Exp. W. J. Hooker, LL. D.' One of these has been donated to our herbarium. Richardon's specimens, recorded as *A. hypoglottis* came, however, from the Saskatchewan River. Besides these, I have seen one from Fifty-mile River, Alaska, collected by Bolton in 1899.

31. ASTRAGALUS AGRESTIS Dougl. As stated above, this name appeared first as a synonym under Hooker's *A. hypoglottis*, the type of which came from the fertile plains of the Red River, Manitoba. See notes under *A. goniatus*. The plant is larger than *A. goniatus* usually is, with larger corolla, pale calyx and long calyx-lobes, and usually longer leaflets. The only similar specimens seen are the following.

MONTANA: St. Ignatius Mission, *MacDougal 298*.

4. CHAETODONTES

This group was established by Dr. Gray, and based on *A. Spaldingii* (originally described as *A. Chaetodon* Torr.) and *A. Lyallii* A. Gray. Later *A. Austinae* A. Gray was added. Jones in his Astragalus included also *A. Brauntoni* Parish, which, however, is not related to the rest. *A. Lyallii*, though somewhat similar in habit to *A. Spaldingii*, has a flattened thin-walled, reflexed pod, which all indicate its relationship to *A. lentiformis* A. Gray and *A. Lemmoni* A. Gray; it has also the small corolla of these species.

32. ASTRAGALUS SPALDINGII A. Gray was originally described as *A. Chaetodon* Torr. As that name had already been used by Bunge, Gray changed it to the present one. It is fairly well understood; its range comprises Washington, Oregon, and western Idaho.

33. ASTRAGALUS AUSTINAE A. Gray was described from specimens collected by Lemmon on Mount Stanford (Castle Peak), Nevada County, California. It is closely related to the preceding but has somewhat the general habit of *Hamosa Andersonii*.

CALIFORNIA: Castle Peak, *Leiberg 5297; Jones* in 1902; *Smiley 480; Lemmon 71;* Placer County, *Sonne 673;* also in 1892.—NEVADA: Mt. Rose, *Heller 9936*.

5. LENTIFORMES

This group is characterized by the small flowers, small, thin-walled, elliptic or lanceolate pod, decidedly flattened, with the upper suture acute, and the sulcus on the lower suture, if any, very narrow. The group is included in *Astragalus* with some hesitation.

34. ASTRAGALUS LYALLII A. Gray was described from specimens collected by Lyall on the Upper Yakima, Washington. It has always been associated with *A. Spaldingii*, but I think it is more closely related to *A. Lemmonii* and *A. lentiformis*. See remarks under CHAETODONTES above.

WASHINGTON: *Whited 343; 97; Vasey 274;* Upper Yakina, *Lyall 8; Henderson 2354; Suksdorf 1816;* Walla Walla, *Wilkes Expedition 543; Brandegee 717;* North Branch of the Columbia, *Wilkes Expedition 543a;* Ellenburg, *Piper 2683; Elmer 366;* Morgan's Ferry, *Suksdorf 282;* Ainsworth, *Tweedy 6151.*—IDAHO: Twin Falls County, *Nelson & Macbride 1713;* Elmora County, *1020;* Glen's Ferry, *Jones* in 1911 (luxuriant form with large fruit; var. *caricinus* M. E. Jones).

35. ASTRAGALUS LENTIFORMIS A. Gray was described from specimens collected by Lemmon in Clover Valley, Sierra Nevada. This species is remarkable on account of its thick woody caudex, and sparse villous pubescence. Jones referred this, as well as the next, to the MICRANTHI. As I have stated in another place, Gray's MICRANTHI was based mainly on *A. Nuttallii* and its relatives, and should properly belong to what Jones called LEPTOCARPI. Jones' MICRANTHI consists mostly of Mexican species, not closely related to *A. lentiformis* and *A. Lemmoni*.

CALIFORNIA: Sierra County, *Lemmon 50*, in part, *73; 537.*

36. ASTRAGALUS LEMMONI A. Gray was also described from specimens collected by Lemmon in Sierra County, California, and is closely related to the preceding, but has shorter stems.

CALIFORNIA: Northern California, *Webber, Lemmon;* Sierra County, *Eastwood 7791; Lemmon 50*, in part, *72, 187;* Kanix Reservation, *Austin & Bruce* in 1897; Siskiyou County, *Greene* in 1876; Chat, *Jones* in 1897.—OREGON: Farwell's Bend, Crook County, *Leiberg 454.*

37. ASTRAGALUS PECKII Piper. This species is related to *A. Lemmoni*, differing mainly in the lower habit, and smaller

acute leaflets. Cusick's specimens were labelled *A. lentiformis* and probably were included by Jones in that species, as he cites specimens from Crook County, Oregon. The species is closer to *A. Lemmoni* than *A. lentiformis*.

OREGON: Crook County, *Peck 9768; Cusick 2818.*

6. BREWERIANI

38. ASTRAGALUS BREWERI A. Gray has no close relative in America, nor as far as I can find, in the Old World. The plant is annual and has some resemblance to *Hamosa tenera* and its allies, but the pod is different, coriaceous, erect, deeply sulcate on the lower suture, and with a stout beak as long as the body itself. The fruit resembles that of *A. Onobrychis* L. of Europe, but its general habit does not. Dr. Gray, who had no mature fruit, placed it next to *A. tener*. Jones transferred it to the DIDYMOCARPI, i.e., the genus *Hesperastragalus* Heller, with which it has no relationship.

CALIFORNIA: Tamalpais, *Brandegee* in 1891; *Eastwood 3164;* Mendocino County, *Abrams 7018; Rattan* in 1884; Sonoma County, *Heller & Brown 5218* in 1902; *Brewer 979* (type); Lake County, *J. P. Tracy 1647; Curran* in 1884; Marine County, *Brewer 955.*

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE
1927–1929

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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